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Morfologia do sistema eferente odorífero metatorácico e filogenia de Pachycorinae (Hemiptera, Heteroptera, Scutelleridae)

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Morfologia do sistema eferente odorífero metatorácico e filogenia de Pachycorinae

(Hemiptera, Heteroptera, Scutelleridae)

LUCIANA WEILER

Aprovada em ______ de ______________________ de ______.

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Everything could have been anything else and it would have had just as much meaning.

Tennessee Williams

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SUMÁRIO

RESUMO

Pachycorinae é o maior da subfamília na região Neotropical, incluindo também sete gêneros com distribuição em todo o continente americano e um gênero com distribuição exclusivamente Neártica. Seus representantes caracterizam-se, historicamente, por apresentar áreas estriadas estridulatórias nos esternitos IV a VII, plectrum nas metatíbias e veia pós-cubital nas asas posteriores. Os pachycoríneos variam em comprimento de 5 a 20 milímetros e são bastante diversificadas na coloração, apresentando cores presumivelmente aposemáticas e criptozóicas. Entretanto, apesar dessas características, Pachycorinae tem recebido pouca atenção e muito pouco se sabe acerca do grupo, sendo que alguns gêneros precisam urgentemente de revisão. Este trabalho traz, pela primeira vez, um estudo detalhado sobre a morfologia externa do sistema odorífero (característica sinapomórfica para Heteroptera), apresentando imagens em microscopia eletrônica de varredura e descrições de 22 dos 24 gêneros atualmente conhecidos da subfamília. As características do sistema odorífero externo de Pachycorinae podem ser utilizadas na distinção entre os gêneros e também em estudos filogenéticos. Também, pela primeira vez, um estudo sobre a filogenia do grupo é realizado com metodologia cladística, baseados em caracteres morfológicos. Testou-se a hipótese de monofilia para Pachycorinae, incluindo 22 dos 24 gêneros (50 espécies), utilizando como grupo externo, 16 espécies representantes das demais subfamílias de Scutelleridae. Pachycorinae foi corroborada parafilética, mas evidenciou-se a existência de um grupo monofilético com 43 espécies das 50 incluídas neste estudo. Todos os gêneros da subfamília que tiveram mais de uma espécie incluída nesse estudo foram recuperados monofiléticos.

INTRODUÇÃO GERAL

A sistemática filogenética visa criar um sistema geral de referência para a diversidade biológica baseado nas relações de parentesco existentes entre os organismos (Hennig 1968). Tal sistema é vantajoso por produzir classificações estáveis e gerar um poder de previsão considerável dentro das Ciências Biológicas (Schuh 2000; Amorim 2002). Atualmente, a cladística é o método de análise filogenética mais amplamente utilizado.

Os insetos da subordem Heteroptera (Hemiptera) compreendem o maior e mais diverso grupo com metamorfose incompleta; e a maioria das 75 famílias ocorre em todos os continentes (exceto Antártica) e em muitas ilhas. Sua história evolutiva e aparente adaptabilidade resultaram em uma grande diversidade estrutural e biológica (Schuh & Slater 1995), incluindo mais de 40.000 espécies descritas (Weirauch & Schuh 2010).

O estudo da Sistemática sobre Heteroptera teve progressos significativos desde a primeira revisão sobre a influência da cladística na classificação de heterópteros de Schuh (1986). Desde então, análises filogenéticas em todos os níveis taxonômicos e o surgimento da sistemática molecular aumentaram consideravelmente a compreensão das relações dentro de Heteroptera e a sua monofilia foi corroborada tanto com dados morfológicos como moleculares (Weirauch & Schuh 2010).

Os pentatomóideos (Hemiptera, Pentatomoidea), popularmente conhecidos como percevejos-do-mato, de distribuição mundial, abrangem 15 famílias. Destas, Pentatomidae tem sido a mais estudada, com a revisão e descrição de inúmeros gêneros e espécies da região Neotropical (e.g., Schwertner *et. al.* 2002; Barcellos & Grazia

2003b, 2008; Grazia & Frey-da-Silva 2003; Grazia & Barcellos 2004, 2005; Fernandes *et al.* 2011; Fernandes & Grazia 2006; Grazia *et al.* 2016a,b; Barão *et al.* 2016; Bianchi *et al.* 2016; Campos *et al.* 2010, 2012). Nas duas últimas décadas, foi introduzida a metodologia cladística para elucidar relações de parentesco entre espécies e gêneros desta família (Grazia 1997; Barcellos & Grazia 2003a; Fortes & Grazia 2005; Campos & Grazia 2006; Bernardes *et al.* 2009; Ferrari *et al.* 2010; Weiler *et al.* 2016).

Composição e histórico de Scutelleridae e Pachycorinae

Contrastando com o grande número de trabalhos já publicados em Pentatomidae, Scutelleridae tem sido um grupo pouco trabalhado, tanto em termos da taxonomia quanto de sua filogenia. A família conta com cerca de 80 gêneros e 450 a 500 espécies (Eger *et al.* 2015), distribuídos por quase todas as regiões biogeográficas, especialmente nos trópicos e subtrópicos. Estes pentatomóideos, que variam de cinco a 20 mm de comprimento, caracterizam-se pelo considerável desenvolvimento do escutelo sobre o abdome, o que lhes confere um aspecto semelhante ao de coleópteros. Os escutelerídeos situam-se entre os percevejos mais vivamente coloridos, às vezes iridescentes, apresentando, em algumas espécies, um polimorfismo surpreendente (Schuh & Slater 1995; Eger *et al.* 2015). Este polimorfismo foi frequentemente causa da descrição de novas espécies para o que na verdade se tratavam apenas de diferentes padrões de coloração apresentados por uma única espécie, exigindo de autores subsequentes o estabelecimento de grande número de sinonímias (Cassis & Vanags 2006).

Apesar destas características, Scutelleridae, curiosamente, tem sido pouco trabalhada (Javahery *et al*. 2000). A última chave publicada para todos os gêneros da família foi a de Schouteden (1904) e o catálogo mundial mais recente foi o de Kirkaldy (1909), embora existam trabalhos e listas mais atuais para faunas regionais (Javahery *et* *al.* 2000). Lattin (1964) forneceu chave para subfamílias, além de discutir a morfologia e biologia da fauna norte-americana. McDonald & Cassis (1984) revisaram a fauna australiana, incluindo chaves para identificação das subfamílias e espécies de Scutelleridae da Austrália. Cassis & Vanags (2006) apresentaram uma ampla revisão do estado de conhecimento sobre escutelerídeos da Austrália, com a redescrição dos gêneros, descrição de novas espécies e listagem de plantas hospedeiras. Segundo esses autores, a maior parte da diversidade do grupo se encontra nas regiões tropicais da Ásia e da América do Sul (Cassis & Vanags 2006). Barcellos *et al.* (2014) apresentaram uma revisão da fauna argentina de Scutelleridae baseada em dados de literatura e de coleções científicas. Eger *et al.* (2015) proveram o primeiro estudo revisivo do conhecimento dos escutelerídeos da região Neotropical, agrupando aspectos gerais de morfologia, biologia e ecologia do grupo, além de fornecer uma chave de identificação para os gêneros neotropicais. No momento, encontra-se em preparação um catálogo mundial de escutelerídeos (J. Eger, com. pes.), do qual se obteve acesso à versão preliminar.

A classificação em nível de subfamília e tribo tem diferido bastante entre os vários autores. Schuh & Slater (1995) reconheceram quatro subfamílias: Odontotarsinae, Pachycorinae, Scutellerinae (com as tribos Elvisurini, Scutellerini e Sphaerocorini) e Eurygastrinae. Cassis & Gross (2002) conferiram o status de subfamília para Elvisurinae, Tectocorinae (para *Tectocoris*), além de reconhecerem Odontotarsinae, Pachycorinae e Scutellerinae. Rider (2016) segue a classificação de Cassis & Gross (2002), acrescentando Odontoscelinae para abrigar, além do gênero-tipo, também *Holonotellus* Horváth, 1890 e *Irochrotus* Amyot & Serville, 1843. A existência dessas diferentes hipóteses de classificação contrasta com a carência de estudos cladísticos para embasar essas propostas.

Para a fauna neotropical, poucos são os trabalhos acerca desta família (Eger 1987, 1990; Paleari 1992; Eger & Lattin 1995; Barcellos *et al.* 2014; Eger *et al.* 2015). No Brasil, os únicos artigos taxonômicos produzidos em Scutelleridae são a revisão de *Agonosoma* Laporte, 1833 (Scutellerinae) por Paleari (1992); a descrição de imaturos de *Galeacius martini* Schouteden, 1904 por Bianchi *et al.* (2011). Os demais trabalhos tratam basicamente de aspectos biológicos de espécies registradas em plantas de interesse econômico, como de *Pachycoris torridus* (Scopoli, 1772), uma das espécies mais frequentemente registradas no Brasil (e.g., Soto & Nakano 2002; Sánchez-Soto *et al.* 2004; Rodrigues *et al.* 2011).

Pachycorinae, atualmente com 24 gêneros e 115 espécies, é a subfamília com o maior número de espécies na região Neotropical, incluindo também alguns gêneros com distribuição em todo o continente americano (Schuh & Slater 1995; Eger *et al.* 2015) Seus representantes caracterizam-se, historicamente, por apresentar áreas estriadas estridulatórias nos esternitos IV a VII, plectrum nas metatíbias e veia pós-cubital nas asas posteriores (Cassis & Vanags 2006; Tsai *et al.* 2011; Eger *et al.* 2015). A falta de conhecimento acerca deste grupo repete o que ocorre para a família como um todo. Apenas para *Tiridates* Stål, 1867 (Eger 1987), *Polytes* Stål, 1867 (Eger 1990) e *Agonosoma* Laporte, 1832 (Paleari 1992) há revisão taxonômica recente. Alguns gêneros com ampla distribuição no Brasil são notadamente carentes de um estudo revisivo como, por exemplo, *Tetyra* Fabricius, 1803, *Symphylus* Dallas, 1851, *Camirus* Stål, 1862, *Crathis* Stål, 1861 e *Lobothyreus* Mayr, 1864. Pachycorinae, originalmente, abrigava dois gêneros africanos, *Hotea* Amyot & Serville, 1843 e *Deroplax* Mayr, 1864.

Carapezza (2009) propõe uma nova subfamília (Hoteinae) para estes gêneros, separando-os com base nas estruturas da genitália interna de macho e fêmea. O autor afirma que o aparelho estridulatório ocorre em espécies de outras subfamílias e comenta ainda que, pela distribuição biogeográfica das espécies de Pachycorinae (Neotropical e/ou Neártica), é incongruente manter *Hotea* e *Deroplax* no mesmo grupo. Entretanto, o autor não utiliza métodos cladísticos nem biogeográficos para sustentar estes argumentos.

Hipóteses sobre a monofilia de Scutelleridae

No histórico do grupo, os escutelerídeos têm sido considerados ora como uma subfamília de Pentatomidae (Stål 1872; Schouteden 1904; Kirkaldy 1909) ora como família de Pentatomoidea (por ex., McDonald & Cassis 1984; Schuh & Slater 1995 e autores subsequentes). A elevação do status para família baseou-se, especialmente, na ausência da estrutura da espermateca duplamente invaginada, verificada em Pentatomidae.

Independentemente de seu status taxonômico, a monofilia de Scutelleridae, com raras exceções (Li *et al*. 2005), tem sido pouco questionada. Na primeira análise cladística realizada para as relações de Pentatomoidea, Gapud (1991) considerou Scutelleridae monofilética, tendo como grupo-irmão Canopidae. Nesse trabalho, os escutelerídeos foram caracterizados pelas seguintes sinapomorfias: (i) dez ou mais veias na membrana das asas anteriores; (ii) gonocoxas II completamente fusionadas; (iii) gonapófises II membranosas, com os ramos secundários fracamente esclerotizados; (iv) gonapófises I membranosas, com diminuta área esclerotizada e (v) espermateca com canal de fecundação alongado e sulcado. Uma das fragilidades da hipótese de Gapud é que, além de ter analisado os caracteres manualmente, o autor os polarizou com base em que o estado mais comum no grupo de estudo deveria ser considerado o estado plesiomórfico.

Fischer (2001) também corroborou a monofilia de Scutelleridae, apoiada por quatro sinapomorfias: escutelo grandemente desenvolvido; primeiras glândulas abdominais em posição lateral; asas posteriores com um hamus (uma pequena veia que surge da extremidade proximal da veia cubital e se curva em direção a R + M) e o cório da asa anterior não-esclerotizado. O autor, contudo, ressalta o grande número de convergências com Pentatomidae. Em sua análise de Scutelleridae, Pachycorinae é o grupo-irmão dos demais escutelerídeos.

Grazia *et al.* (2008) realizaram análises cladísticas de Pentatomoidea, empregando 57 caracteres morfológicos e 3500 pares de bases de DNA. Os autores apresentaram cladogramas baseados apenas em morfologia, apenas em dados moleculares e englobando ambos os tipos de caracteres (evidência total). Além da monofilia de Pentatomoidea, os resultados também apoiaram de forma consistente a monofilia de Scutelleridae, em todas as análises. Entretanto, a posição de Scutelleridae em Pentatomoidea variou com os diferentes conjuntos de caracteres empregados, mas geralmente situando-se em uma posição mais basal em relação à Pentatomidae.

Tsai *et al.* (2011) questiona os resultados de Grazia *et al.* (2008), enumerando e discutindo os quatro estados de caracteres morfológicos que suportam a monofilia de Scutelleridae: tubérculos anteníferos em posição ventral parcialmente encobertos pelas placas mandibulares; 2 + 2 tricobótrios abdominais posicionados transversal ou diagonalmente posteriores aos espiráculos; ausência de triangulin e áreas circundantes a abertura da espermateca providas de um longo e sulcado esclerito. Os autores argumentam que os três primeiros caracteres citados são homoplásticos, plesiomórficos ou simplesiomórficos e que apenas a quarta característica poderia ser um sinal da monofilia da família. Entretanto, tal característica é ausente em alguns membros além de estruturas similares serem encontradas em famílias de pentatomóideos, sendo necessária uma investigação mais profunda e com amostragem mais ampla para ser conclusiva.

Wu et al. (2016) analisaram a estrutura secundária de rRNA de 15 famílias de Pentatomoidea e os resultados mostraram uma parafilia em Scutelleridae. Entretanto, os autores incluíram apenas três espécies (*Hotea curculionoides* Herrich-Schäffer, 1836, *Eurygaster testudinaria* (Geoffroy, 1785) e Odontoscelis fuliginosa (Linnaeus, 1761) e afirmam que a posição de *H. curculionoides* entre as espécies de Cyrtocoridae deve-se, provavelmente, à atração de ramos longos, uma vez que a estrutura encontrada na família em questão é única entre os pentatomóideos.

Ademais, Pachycorinae, morfologicamente a mais heterogênea e controversa subfamília, foi completamente excluída das análises morfológica e moleculares de Grazia *et al.* (2008). Tsai *et al.* (2011) concluem que a monofilia de Scutelleridae é fracamente suportada por caracteres morfológicos e que os dados moleculares são muito fragmentados para que uma hipótese razoável seja elaborada.

Hipóteses sobre a monofilia e relações de Pachycorinae

A análise de Fischer (2001) para as relações em Pachycorinae hipotetizou a monofilia do grupo, baseada em três sinapomorfias: presença de áreas estridulatórias abdominais em ambos os sexos; de plectrum nas tíbias posteriores e de veia pós-cubital nas asas posteriores. Em sua análise, os dois gêneros africanos *Hotea* e *Deroplax* são grupos-irmãos e ambos, por sua vez, formam o grupo-irmão dos demais gêneros analisados. O autor, porém, utilizou apenas 14 dos então 26 gêneros que compunham a subfamília, além de sua análise não ter se baseado nos pressupostos cladísticos e não seguir a metodologia cladística.

Apesar da subfamília ser primariamente caracterizada pela presença das áreas estridulatórias no ventre abdominal, esta característica não é exclusiva de Pachycorinae, ocorrendo também, pelo menos, em Hoteinae e Odontotarsinae. Uma vez que o grupo apresenta alta diversidade em diversos outros aspectos e as genitálias masculinas e femininas não apresentam um padrão, sua monofilia é questionável (Tsai *et al.* 2011).

Não há, portanto, estudos sobre a sistemática e filogenia do grupo que tenham metodologia objetiva, explícita e falseável. Todas as propostas de classificação, até então, são fundamentadas em observações pessoais dos pesquisadores, sem uma análise imparcial sobre os dados.

Estrutura da Tese

Esta tese está estruturada em formato de artigos, que compõem dois capítulos. No Capítulo I estudamos a morfologia do sistema eferente odorífero metatorácico da subfamília Pachycorinae, tendo 22 dos 24 gêneros conhecidos atualmente amostrados. No Capítulo II realizamos uma análise filogenética para testar a monofilia da subfamília Pachycorinae, utilizando caracteres morfológicos e pesagem implícita de caracteres. Como grupo externo, representantes das demais subfamílias de Scutelleridae foram incluídos na matriz de dados.

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CAPÍTULO I[1]

Morphology of the external scent efferent system of Neotropical shield bugs (Hemiptera: Scutelleridae: Pachycorinae)

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Abstract

The metathoracic scent glands are characteristic of the true bug suborder Heteroptera and are known to have defensive, sexual and aggregation roles, among others. The morphology of external cuticular structures (ESES) associated with these glands has taxonomic and phylogenetic importance. These structures have been documented previously in four of the eight Scutelleridae subfamilies. In this work we investigate them in detail in 22 genera of the New World subfamily Pachycorinae using scanning electron microscopy. We report five general types of ESES in pachycorine: i. enlarged evaporatorium and well-developed peritreme; ii. well-developed evaporatorium and poorly developed or obsolete peritreme; iii. reduced evaporatorium and small or

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obsolete peritreme; iv. reduced evaporatorium on mesepimeron and elongate peritreme; v. enlarged evaporatorium and elongate peritreme. Our results are in contradistinction to previous accounts of the external scent efferent system for the Pachycorinae which have been reported as being poorly developed. The Pachycorinae patterns do not support Schaefer's hypothesis that there is a correlation between degree of development of the external metathoracic structures and way of life. We also demonstrate that these structures are of systematic importance in the Pachycorinae.

KEYWORDS. Metathoracic glands, morphology, New World, jewel bugs, taxonomy, scanning electron microscopy.

Introduction

The metathoracic gland (MTG) is an exocrine system that is ubiquitous in the suborder Heteroptera (Insecta: Hemiptera). Across terrestrial bugs (Geocorisae) the main function of these glands is defensive, but they also are known to produce sexual, alarm and aggregation signals (Staddon 1979, Aldrich 1988, Millar et al. 2002). The exocrine system includes the glands themselves, often with reservoirs, internal conducting canals, and an external efferent system (ESES). Systematists have found that the variation of the external efferent system is indicative of phylogenetic relationships and can be used to differentiate taxa at multiple levels of the taxonomic hierarchy (e.g., Carayon 1955, 1971, Davidová-Vilímová et al. 2000, Schaefer 2004, Weirauch 2006, Schaefer and Ahmad 2008, Cassis and Schuh 2012). The MTGs of several families of the heteropteran Pentatomoidea have received terminological standardization (Kment and Vilímová 2010b) and comparative morphological study, using scanning electron microscopy (e.g., Kment and Vilímová 2010a, Kment et al. 2012, Parveen et al. 2014, Barão et al. *in press*). Schaefer (1972) hypothesized that differences in the MTG are driven by ecological factors; for example, he proposed that arboreal trichophoran bugs (Pentatomomorpha: Trichophora) have less developed MTGs than ground-dwelling or herbaceous feeding taxa.

MTGs have been found to have taxonomic importance in the superfamily Pentatomoidea and can be used for genus-level discrimination (e.g., Wood and McDonald 1984; Kment 2008, 2015; Tsai et al. 2011; Barcellos et al. 2014; Eger et al. 2015; Grazia et al. 2015; Schwertner and Grazia 2015) and phylogenetic inference (Cassis and Vanags 2006, Kment & Vilímová 2010a). However, structures of the external scent efferent system (ESES) have been mostly documented with short characterizations included in species and genus descriptions (e.g., Eger 1987, Lis 2003, Matesco and Grazia 2013, Garbelotto et al. 2014, Grazia et al. 2016).

In this study we focus on the ESES in the family Scutelleridae, which are commonly called shield or jewel bugs; they comprise both bright (putatively aposematic) and dull brown taxa. The ESES of scutellerids have been described by numerous authors using light (e.g., McDonald and Cassis 1984, Schouteden 1904, Eger 1990, Tsai et al. 2011) and electron microscopy (e.g., Cassis and Vanags 2006, Kment and Vilímova 2010b, Parveen et al. 2014). Schouteden (1904) used states of the ostiole and peritreme of the ESES to distinguish between scutellerid tribes and genera (family treated as a subfamily of Pentatomidae). Parveen et al. (2014) evaluated variation of the ESES of the scutellerid subfamilies Elvisurinae, Eurygastrinae, Hoteinae, and Scutellerinae. Cassis and Vanags (2006) described and provided electron micrographs of most Australian scutellerid genera, including the enigmatic species *Morbora australis* Distant, 1899 (Odontotarsinae) and *Tectocoris diophthalmus* (Thunberg, 1783) (Tectocorinae), and of the biological control agent *Agonosoma trilineatum* (Fabricius,

1781) (Pachycorinae). The ESES is unexplored in the scutellerid subfamily Odontoscelinae and in many genera of the other subfamilies.

The Neotropical scutellerid fauna is one of the most speciose in the world, yet is the poorest known, and most species belong to the New-World subfamily Pachycorinae, comprising 115 species in 24 genera (Eger et al. 2015). Recent taxonomic revisions of the pachycorines made little mention of the ESES (e.g., Eger 1987, 1990, Carapezza 2009, Barcellos et al. 2014) and Eger et al. (2015) described the ESES of 14 genera of Pachycorinae, at a gross level using light microscopy.

Here, we aim to describe in detail the external scent efferent system of 22 genera of Pachycorinae, using scanning electron microscopy. These data provide a novel source of morphological information on the Pachycorinae, which can aid in genus-group identification and in any future phylogenetic studies.

Material and Methods

The following species belonging to 22 genera of Pachycorinae were studied under SEM: *Acantholomidea porosa* (Germar, 1839) (Fig. 1a), *Agonosoma flavolineata* Laporte, 1832 (Fig. 1b), *Ascanius hirtipes* (Herrich-Schäffer, 1836) (Fig. 1c), *Camirus moestus* (Stål, 1862) (Fig. 1d), *Chelycoris haglundi* (Montandon, 1895) (Fig. 1e), *Chelyschema trinotata* (Walker, 1867) (Fig. 1f), *Coptochilus ferrugineus* Amyot & Serville, 1843 (Fig. 1g), *Crathis ansata* (Distant, 1889) (Fig. 1h), *Diolcus irroratus* (Fabricius, 1775) (Fig. 1i), *Dystus puberulus* Stål, 1862 (Fig. 1j), *Galeacius martini* Schouteden, 1904 (Fig. 1k), *Homaemus aeneifrons* (Say, 1824) (Fig. 1l), *Lobothyreus lobatus* (Westwood, 1837) (Fig. 1m), *Misippus spinolae* (Signoret, 1863) (Fig. 1n), *Orsilochides variabilis* (Herrich-Schäffer, 1837) (Fig. 1o), *Pachycoris torridus* (Scopoli, 1772) (Fig. 1p), *Polytes lineolatus* (Dallas, 1851) (Fig. 1q), *Sphyrocoris* *obliquus* (Germar, 1839) (Fig. 1r), *Stethaulax marmorata* (Say, 1831) (Fig. 1s), *Symphylus ramivitta* Walker, 1838 (Fig. 1t), *Tetyra antillarum* Kirkaldy, 1909 (Fig. 1u), *Tiridates rubrocinctus* (Herrich-Schäffer, 1837) (Fig. 1v). Only the pachycorine genera *Ephynes* Stål, 1867 and *Testrina* Walker, 1867 were not investigated because they are known only from type specimens. Under light microscopy we found few differences in the congeners of the above genera. A list of examined specimens is available in Online Resource 1. The specimens used in this study were borrowed from the following institutions: DARC, David A. Rider Collection, North Dakota State University, North Dakota, United States of America; DZUP, Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Paraná, Brazil; JEEC, Joseph Eger Collection, Dow AgroSciences, Florida, United States of America; MCNZ, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Rio Grande do Sul, Brazil; MGAP, Museu Anchieta, Rio Grande do Sul, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; UFRG, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Rio Grande do Sul, Brazil; USNM, National Museum of Natural History, Washington D.C. United States of America.

Tegumentary ultrastructure was studied using scanning electron microscopy (SEM) JEOL JSM6060 at the Centro de Microscopia e Microanálise of UFRGS and HITACHI TM3000 Tabletop Scanning Electron Microscope at Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences of UNSW. Meso- and metapleuron of pinned specimens were removed, cleaned manually with forceps and fine tipped brush and isopropyl alcohol, kept submerged in contact lens solution Renu® for 48 h, and then agitated in an ultrasonic bath (5.400 kHz) with water and detergent solution for 45 seconds. Following this procedure, the meso- and metapleuron were dehydrated at 50 °C for 48 h, sputter coated with carbon and gold and observed by SEM. We follow the terminology of external scent efferent system proposed by Carayon (1971) and Kment and Vilímová (2010b).

Results

Acantholomidea porosa **(Germar)**

(Figures 1a, 2)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 2a); ostiole elliptical, oriented ventrally, not visible in lateral view; lateral and posterior margins of ostiolar plate leveled with remaining of metapleuron; peritreme small, directed posterolaterally, elevated from surrounding pleuron(Fig. 2b), median furrow obsolete; peritremal surface covered with rugose, scale-like microsculptures (Fig. 2c). Evaporatorium poorly developed on meso- and metapleuron; on metapleuron, evaporatorium surrounding ostiole and peritreme and along the metapleural margin of spiracle, but not reaching between coxal cavities, outer margin of metapleural evaporatorium sigmoid; on mesopleuron, developed on mesepimeron along the spiracular margin and on lateral margin of mesopleuron; evaporatorium punctate (Fig. 2d); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle narrow; processes of the filter system of irregular diameter, processes spiny and connected to each other by lateral expansions (Fig. 2e).

Agonosoma flavolineata **Laporte**

(Figures 1b, 3)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 3a); ostiole elliptical, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme groove-shaped, long, directed posterolaterally and apically curved anteriorly, parallel to surrounding pleuron (Fig. 3b), median furrow well-developed; peritremal surface covered with smooth, flap-like microsculptures (Fig. 3c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium covering most of the ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex and elevated; on mesopleuron, well-developed on mesepimeron; evaporatorium with several minute sensilla (Fig. 3d); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of irregular diameter, processes spiny (Fig. 3e).

Ascanius hirtipes **(Herrich-Schäffer)**

(Figures 1c, 4)

Ostiole in the middle of on metapleuron (Fig. 4a); ostiole elliptical, oriented ventrolaterally, not visible in lateral view; posterior margin of ostiolar plate elevated; peritreme spout-shaped, directed posterolaterally, elevated and parallel to surrounding pleuron (Fig. 4b), median furrow well-developed; peritremal surface covered with scale-like microsculptures (Fig. 4c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium covering most of the ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium concave; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 4d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny (Fig. 4e).

Camirus moestus **(Stål)**

(Figures 1d, 5)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 5a); ostiole guttiform, oriented ventrally, not visible in lateral view; lateral and posterior margins of ostiolar plate leveled with remaining of metapleuron; peritreme small, elevated from surrounding pleuron, directed posterolaterally (Fig. 5b), median furrow obsolete; peritremal surface covered with conical, scale-like microsculptures (Fig. 5c). Evaporatorium poorly developed on meso- and metapleuron; on metapleuron, evaporatorium surrounding ostiole and peritreme and along the metapleural margin of spiracle, and reaching between coxal cavities, outer margin of metapleural evaporatorium sigmoid; on mesopleuron, developed on mesepimeron along the spiracular margin and on lateral margin of mesopleuron; evaporatorium punctate (Fig. 5d), punctures bearing long seta; mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny and connected to each other by few lateral expansions (Fig. 5e).

***Chelycoris haglundi* (Montandon)**

(Figures 1e, 6)

Ostiole in the middle of metapleuron (Fig. 6a); ostiole round, oriented ventrally, not visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed posterolaterally, elevated and parallel to surrounding pleuron (Fig. 6b), median furrow well-developed; peritremal surface covered with ridged, scale-like microsculptures (Fig. 6c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium covering most of ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium straight and elevated; on mesopleuron, well-developed on mesepimeron, reaching posterolateral angle of mesopleuron but not extending on mesopleural lateral margin; evaporatorium punctate (Fig. 6d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with setae; processes of the filter system of conical, processes spiny (Fig. 6e).

***Chelyschema trinotata* (Walker)**

(Figures 1f, 7)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 7a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme reduced, directed laterally (Fig. 7b), median furrow obsolete; peritremal surface smooth (Fig. 7c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium covering most of ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium with several minute sensilla (Fig. 7d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of irregular diameter, processes spiny (Fig. 7e).

***Coptochilus ferrugineus* Amyot & Serville**

(Figures 1g, 8)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 8a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed laterally (Fig. 8b), median furrow well-developed; peritremal surface with cylindrical microsculptures

(Fig. 8c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium covering most of ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 8d) and with several minute sensilla (Fig. 8e); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter, processes spiny and connected to each other by few lateral expansions (Fig. 8f).

Crathis ansata **(Distant)**

(Figures 1h, 9)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 9a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral margin of ostiolar plate elevated; peritreme ruga-shaped, directed laterally reaching anterolateral margin of ostiolar plate (Fig. 9b), median furrow developed basally; peritremal surface with scattered, spike-like microsculptures and minute sensilla (Fig. 9c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium straight; on mesopleuron, well-developed on mesepimeron; evaporatorium with several minute sensilla (Fig. 9d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny (Fig. 9e).

Diolcus irroratus **(Fabricius)**

(Figures 1i, 10)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 10a); ostiole round, oriented ventrolaterally, visible in lateral view; lateral margin of ostiolar plate elevated; peritreme reduced, directed laterally (Fig. 10b), median furrow obsolete; peritremal surface with cylindrical microsculptures (Fig. 10c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium with several minute sensilla (Fig. 10d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle narrow; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter and conical, processes smooth (Fig. 10e).

Dystus puberulus **Stål**

(Figures 1j, 11)

Ostiole in the middle of metapleuron (Fig. 11a); ostiole elliptic, oriented posterolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed anterolaterally (Fig. 11b), median furrow obsolete; peritremal surface reticulate, with elevated ridges (Fig. 11c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium straight; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 11d) and bearing setae (Fig. 11e); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny (Fig. 11f).

Galeacius martini **Schouteden**

(Figures 1k, 12)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 12a); ostiole round, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme groove-shaped, directed laterally and apically curved anteriorly, parallel to surrounding pleuron (Fig. 12b), median furrow well-developed; peritremal surface with rugose, scale-like microsculptures (Fig. 12c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 12d); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of irregular diameter, processes spiny (Fig. 12e).

Homaemus aeneifrons **(Say)**

(Figures 1l, 13)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 13a); ostiole elliptic, oriented ventrally, not visible in lateral view; lateral and posterior margins of ostiolar plate leveled with remaining of metapleuron; peritreme groove-shaped, golf-club-like, directed laterally and apically curved anteriorly, parallel to surrounding pleuron (Fig. 13b), median furrow well-developed; peritremal surface smooth with spike-like microsculptures along the median furrow (Fig. 13c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and tapered towards coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, reduced on mesepimeron; evaporatorium punctate (Fig. 13d); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle narrow; processes of the filter system of irregular diameter, some bifurcate apically, processes spiny (Fig. 13e).

Schaefer (1972) reports that *Homaemus aeneifrons* has a large evaporatorium and a poorly developed peritreme. However, we conclude that his observations are based on misidentified specimens, as all *Homaemus* species have a well-developed clavate peritremal groove.

Lobothyreus lobatus **(Westwood)**

(Figures 1m, 14)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 14a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme ruga-shaped, directed laterally reaching the anterolateral margin of the ostiolar plate (Fig. 14b), median furrow developed basally; peritremal surface with rugose, scale-like microsculptures (Fig. 14c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 14e); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny (Fig. 14f).

Misippus spinolae **(Signoret)**

(Figures 1n, 15)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 15a); ostiole round, oriented laterally, visible in lateral view; lateral and posterior margins of ostiolar plate leveled with remaining of metapleuron; peritreme obsolete (Fig. 15b), median furrow obsolete. Evaporatorium poorly developed on meso- and metapleuron; on metapleuron, evaporatorium surrounding ostiole, along the metapleural margin of spiracle, and reaching between coxal cavities; on mesopleuron, developed on mesepimeron along the spiracular margin and not reaching lateral margin of mesopleuron; evaporatorium punctate (Fig. 15c); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes smooth and connected to each other by lateral expansions (Fig. 15e).

Orsilochides variabilis **(Herrich-Schäffer)**

(Figures 1o, 16)

Ostiole in the middle of metapleuron (Fig. 16a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed laterally (Fig. 16b), median furrow obsolete; peritremal surface reticulate, with elevated ridges (Fig. 16c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium concave; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 16d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter, processes spiny (Fig. 16f).

***Pachycoris torridus* (Scopoli)**

(Figures 1p, 17)

Ostiole in the middle of metapleuron (Fig. 17a); ostiole guttiform, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed laterally (Fig. 17b), median furrow obsolete; peritremal surface with disorganized, elevated ridges (Fig. 17c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 17d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter, processes spiny (Fig. 17f).

***Polytes lineolatus* (Dallas)**

(Figures 1q, 18)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 18a); ostiole round, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme obsolete (Fig. 18b), median furrow obsolete. Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium with minute sensilla (Fig. 18c); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of irregular diameter, processes spiny (Fig. 18d).

Sphyrocoris obliquus **(Germar)**

(Figures 1r, 19)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 19a); ostiole elliptic, oriented ventrolaterally, not visible in lateral view; peritreme groove-shaped, smoking-pipe-like, directed laterally and appically ample and curved anteriorly, parallel to surrounding pleuron (Fig. 19b), median furrow well-developed; peritremal surface smooth with spike-like microsculptures and setae along the median furrow (Fig. 19c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and tapered towards coxal cavities; reduced on mesopleuron; evaporatorium punctate and setose (Fig. 19d); mushroom bodies irregular, alveoli with few trabeculae. Metathoracic spiracle narrow; metapleural margin of spiracle with several setae; processes of the filter system of irregular diameter, some bifurcate apically, processes spiny (Fig. 19e).

Stethaulax marmorata **(Say)**

(Figures 1s, 20)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 20a); ostiole elliptic, oriented ventrolaterally, visible in lateral view; lateral margin of ostiolar plate elevated; peritreme groove-shaped, directed laterally and apically curved anteriorly, parallel to surrounding pleuron (Fig. 20b), median furrow well-developed; peritremal surface with scale-like microsculptures (Fig. 20c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron;

evaporatorium punctate (Fig. 20d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter, processes spiny (Fig. 20e).

***Symphylus ramivitta* Walker**

(Figures 1t, 21)

Ostiole closer to metacoxal cavity than to lateral margin of metapleuron (Fig. 21a); ostiole round, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme directed laterally, parallel to surrounding pleuron (Fig. 21b), median furrow developed basally; peritremal surface with scale-like microsculptures (Fig. 21c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium deeply punctate (Fig. 21a, d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; processes of the filter system of regular diameter, processes spiny and connected to each other by lateral expansions (Fig. 21e).

***Tetyra antillarum* Kirkaldy**

(Figures 1u, 22)

Ostiole in the middle of metapleuron (Fig. 22a); ostiole elliptic, oriented posterolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate elevated; peritreme spout-shaped, directed laterally (Fig. 22b), median furrow obsolete; peritremal surface reticulate, with elevated ridges (Fig. 22c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium with minute sensilla (Fig. 22d) and punctate (Fig. 22e); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle wide; metapleural margin of spiracle with several setae; processes of the filter system of regular diameter, processes spiny (Fig. 22f).

Tiridates rubrocinctus **(Herrich-Schäffer)**

(Figures 1v, 23)

Ostiole in the middle of metapleuron (Fig. 23a); ostiole round, oriented ventrolaterally, visible in lateral view; lateral and posterior margins of ostiolar plate leveled with remaining of metapleuron; peritreme spout-shaped, directed laterally (Fig. 23b), median furrow developed basally; peritremal surface with spike-like microsculptures (Fig. 23c). Evaporatorium well-developed on meso- and metapleuron; on metapleuron, evaporatorium completely covering ostiolar plate and reaching between coxal cavities, outer margin of metapleural evaporatorium convex; on mesopleuron, well-developed on mesepimeron; evaporatorium punctate (Fig. 23d); mushroom bodies irregular, alveoli with several trabeculae. Metathoracic spiracle narrow; processes of the filter system of regular diameter, processes spiny (Fig. 23e).

Discussion

Pachycorinae genera have been characterized as having a weakly developed ESES (Schouteden 1904, Eger 1990, Cassis and Vanags 2006). In contrast, we found that the subfamily has a greatly enlarged evaporatorium and a small to moderately sized peritreme, particularly in comparison to those observed in other subfamilies (e.g., Cassis and Vanags 2006, Parveen et al. 2014).

We found five general patterns of the external scent efferent system within Pachycorinae:

1) Enlarged evaporatorium and relatively well-developed peritreme (*Agonosoma*, *Ascanius*, *Chelycoris*, *Coptochilus*, *Dystus*, *Galeacius*, *Orsilochides*, *Pachycoris*, *Tetyra*, *Tiridates*, *Stethaulax*, and *Symphylus*): the evaporatorium is well-developed on meso- and metapleuron, and the length of peritreme is at least twice the diameter of the ostiole;

2) enlarged evaporatorium and poorly developed or obsolete peritreme (*Chelyschema*, *Diolcus*, and *Polytes*): the evaporatorium is well-developed on meso- and metapleuron, and the length of peritreme is at most as long as the ostiole or obsolete;

3) reduced evaporatorium and small or obsolete peritreme (*Acantholomidea*, *Camirus*, and *Misippus*): the evaporatorium is poorly developed on meso- and metapleuron, restricted to the margins of spiracle, the peritremal surface is small and blade-like or obsolete;

4) reduced evaporatorium on mesepimeron and elongate peritreme (*Homaemus* and *Sphyrocoris*): the evaporatorium is well-developed on metapleuron and reduced on mesepimeron, the peritreme is greatly developed, clavate shaped;

5) enlarged evaporatorium and elongate peritreme (*Crathis* and *Lobothyreus*): the evaporatorium is well-developed on meso- and metapleuron, the peritremal surface is very long and narrow.

Characteristics of the ESES are most informative for taxonomy at the generic level for Scutelleridae (Cassis and Vanags 2006) with congeners often having very similar ESES morphology (Tsai et al. 2011, Parveen et al. 2014). In particular, the peritremal shape has been used by Schouteden (1904), Barcellos et al. (2014), Eger (1987) and Eger et al. (2015) in their identification keys of Pachycorinae genera. We also found that Pachycorinae genera can be easily recognized by ESES features, aside from *Crathis* and *Lobothyreus*.

Carayon (1971) suggested that in Heteroptera the external elements of metathoracic glands have differentiated more recently compared with associated internal elements, especially the evaporatorium. Based on this assumption, Parveen et al. (2014) suggested that the ESES is not suitable for phylogenetic analyses because of probable high levels of homoplasy. Elsewhere in the Heteroptera, the ESES has been found to have phylogenetic signal, particularly in the infraorder Cimicomorpha (e.g., Drake and Davis 1960, Cassis 1995, Schuh et al. 2009, Weirauch 2008). In contrast, in the Pentatomoidea, characters of the ESES have been rarely coded for phylogenetic analyses (e.g. Gapud 1991, Hasan and Kitching 1993, Kment and Vilímová 2010a, Roell and Campos 2015).

Schaefer (1972) investigated the ESES in trichophoran Heteroptera and proposed that characters of the ESES are correlated with habitat and lifestyle, replicated in independent clades. We sought to investigate this in pachycorines by documenting their host-plants and habitats based on the literature (Online Resource 2; also, Eger et al. 2015). We found that the ESES of pachycorines is mostly not congruent with Schaefer’s hypotheses, which is true for other heteropteran taxa (e.g. Aldrich 1988, Kment and Vilímová 2010a, Parveen et al. 2014). In cases where there are suggestions of a correlation, a phylogeny is lacking that would enable an appropriate test (e.g. *Polytes lineolatus* is in alignment with Schaefer’s prediction that aposematic, arboreal bugs would have a poorly developed ESES; and *Diolcus* spp. are consistent with Schaefer’s hypothesis that ‘undergrowth’ inhabiting taxa would have a reduced peritreme and enlarged evaporatorium).

In summary, the external scent efferent system of Pachycorinae can reliably aid in generic identification and because there are five general patterns found it is likely to be a useful character system for phylogenetic inference. The study of the ESES and its possible correlation with lifestyle is worthy of investigation, but pachycorine biology and habitats are at present too poorly known, and phylogenies are lacking, which is required to test any ecomorphological hypothesis.

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Figures

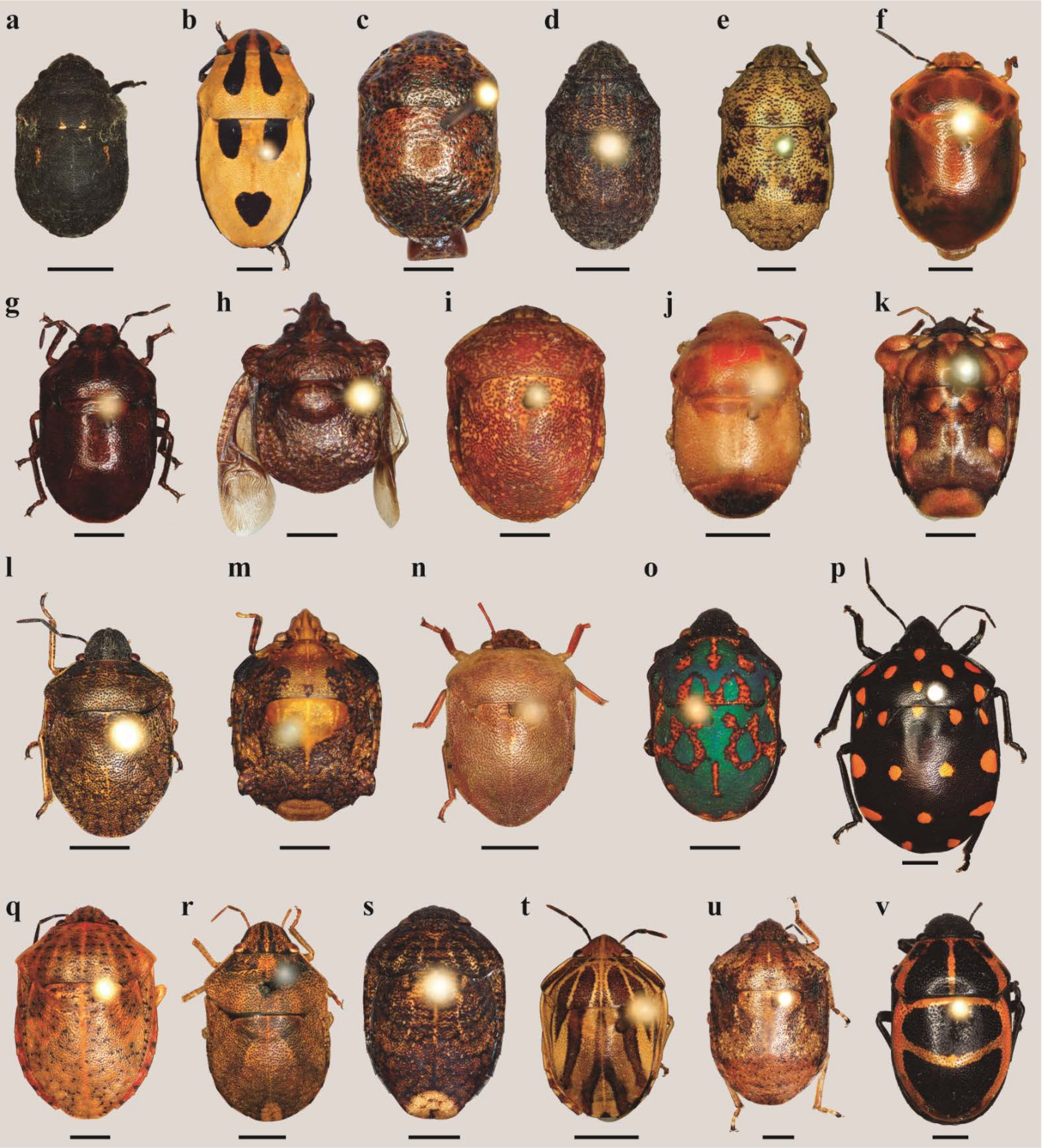

Fig. 1 Dorsal facies of representatives of Pachycorinae genera. (a) *Acantholomidea porosa*. (b) *Agonosoma flavolineata*. (c) *Ascanius hirtipes*. (d) *Camirus moestus*. (e) *Chelycoris haglundi*. (f) *Chelyschema trinotata*. (g) *Coptochilus ferrugineus*. (h) *Crathis ansata*. (i) *Diolcus irroratus*. (j) *Dystus puberulus*. (k) *Galeacius martini*. (l) *Homaemus aeneifrons*. (m) *Lobothyreus lobatus*. (n) *Missipus spinolae*. (o) *Orsilochides*

variabilis. (p) *Pachycoris torridus*. (q) *Polites lineolatus*. (r) *Sphyrocoris obliquus*. (s) *Stethaulax marmorata*. (t) *Symphylus ramivitta*. (u) *Tetyra antillarum*. (v) *Tiridates rubrocinctus*. Bars: 1 mm

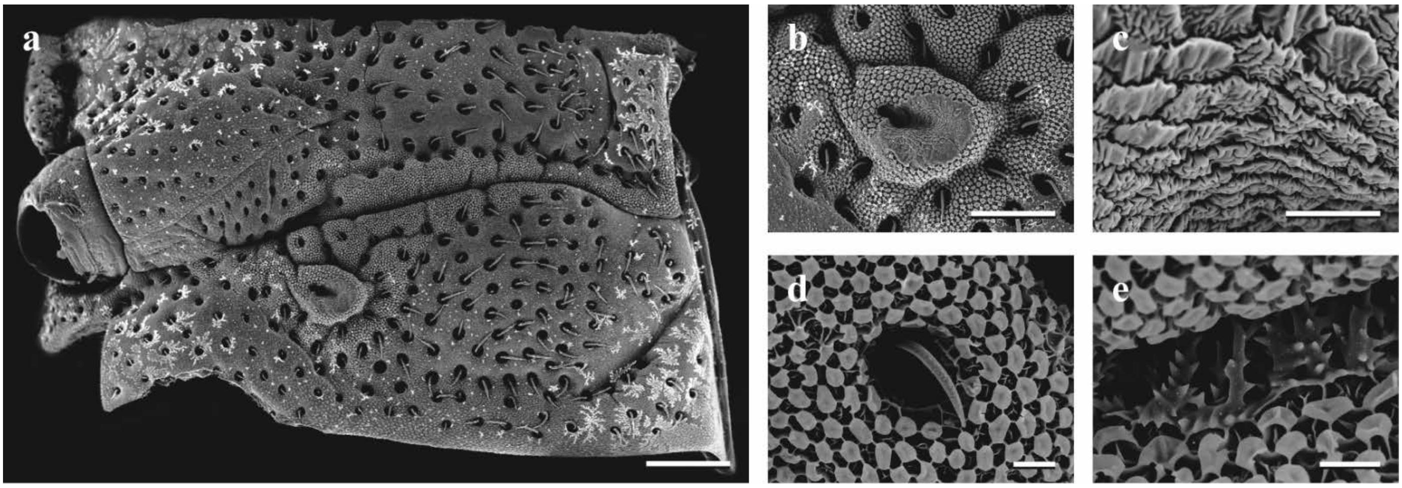

Fig. 2 External scent efferent system of *Acantholomidea porosa*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 200 µm; (b) 100 µm; (c-e) 10 µm

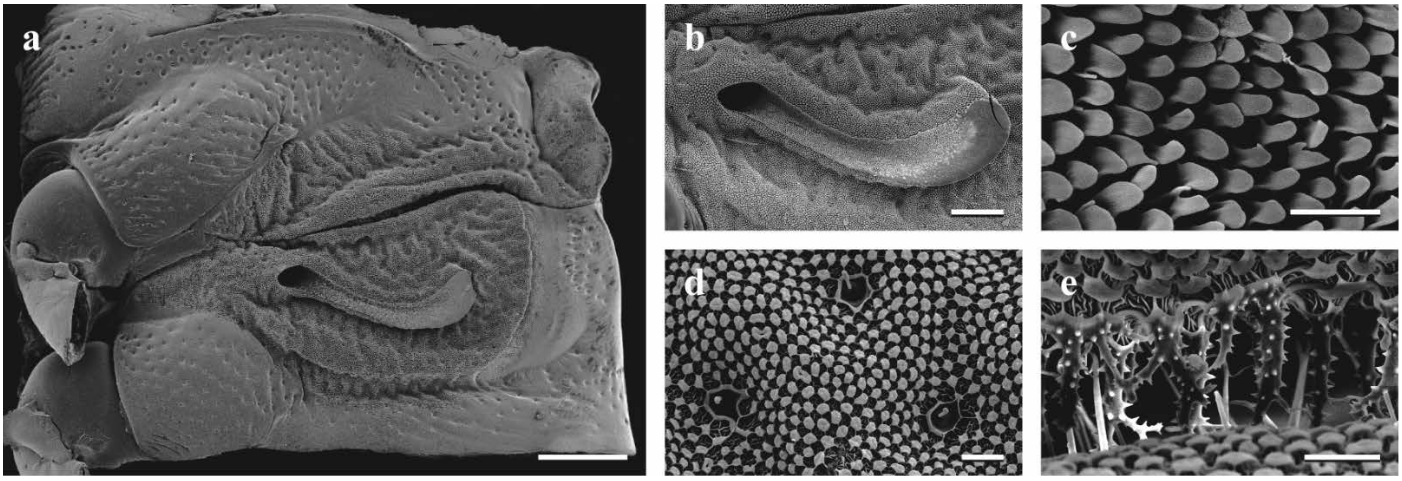

Fig. 3 External scent efferent system of *Agonosoma flavolineata*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c) 10 µm; (d-e) 20 µm

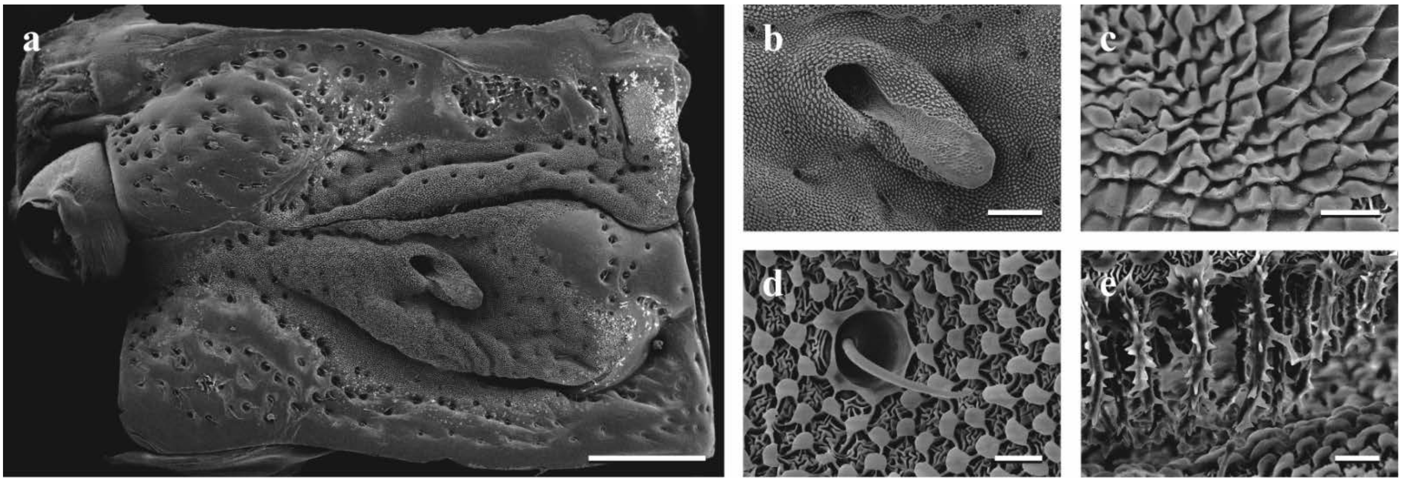

Fig. 4 External scent efferent system of *Ascanius hirtipes*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-e) 10 µm

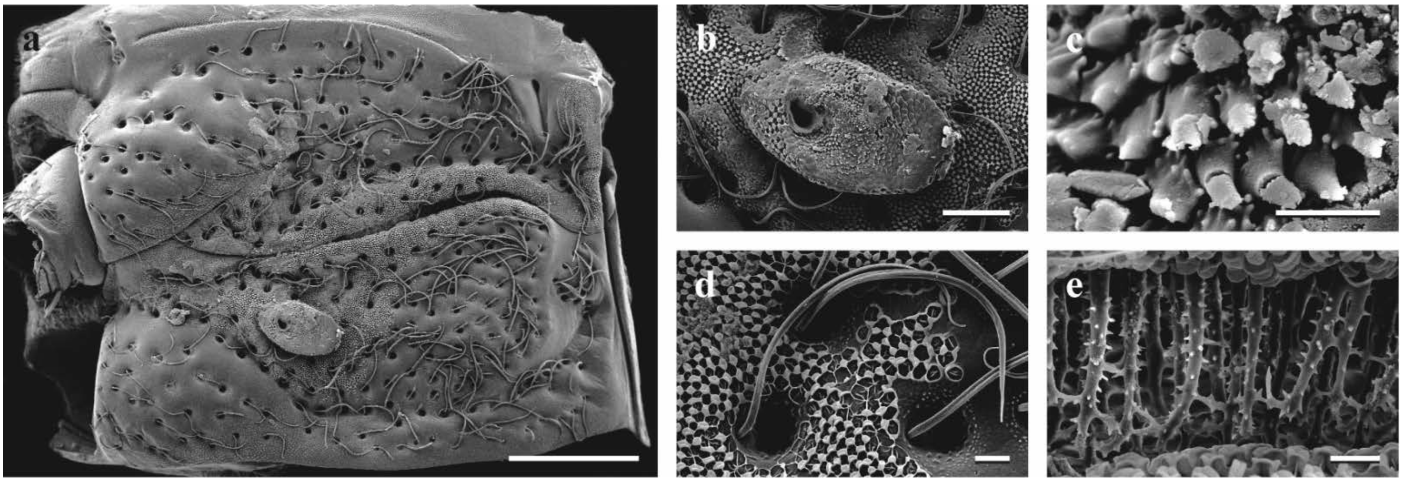

Fig. 5 External scent efferent system of *Camirus moestus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-e) 10 µm

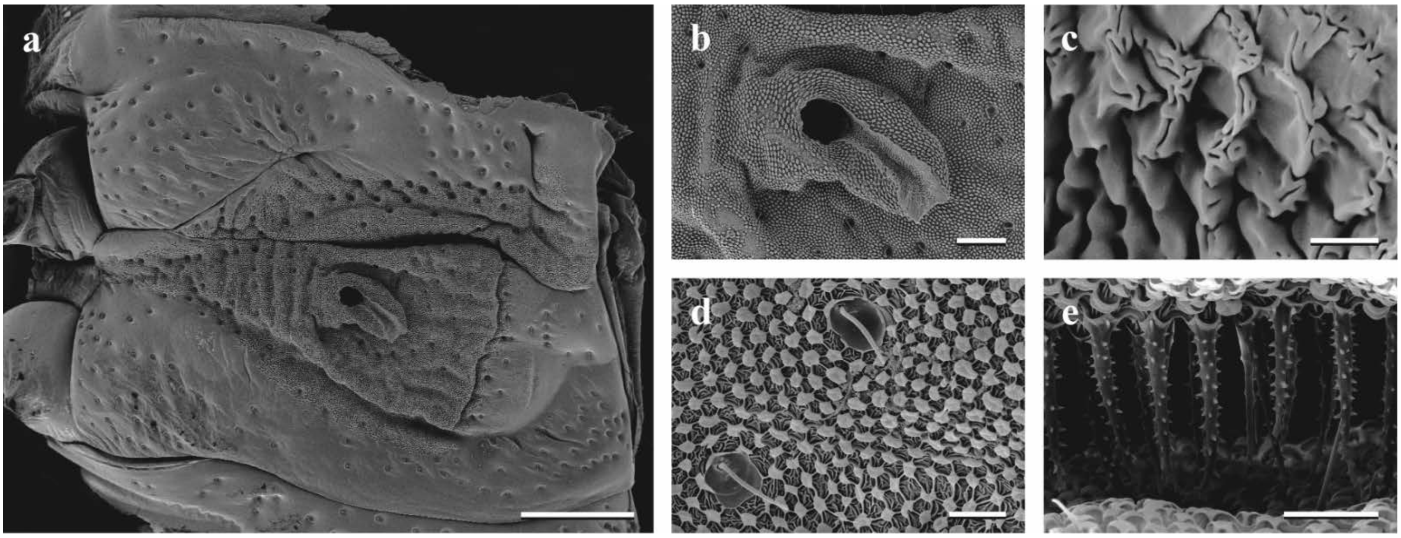

Fig. 6 External scent efferent system of *Chelycoris haglundi*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c) 5 µm; (d-e) 20 µm

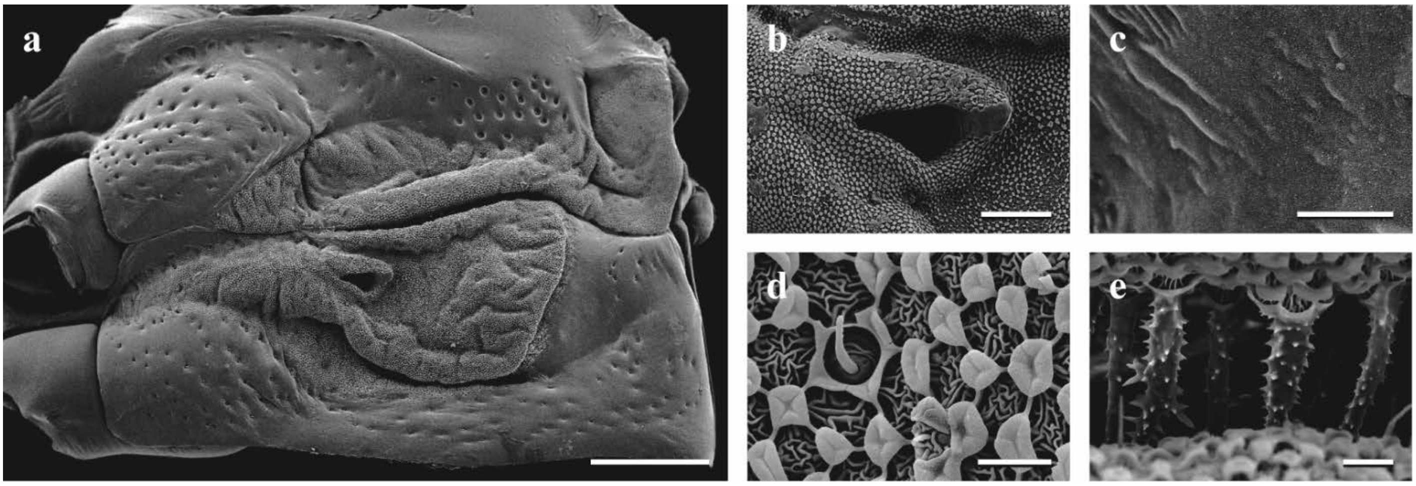

Fig. 7 External scent efferent system of *Chelyschema trinotata*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-e) 10 µm

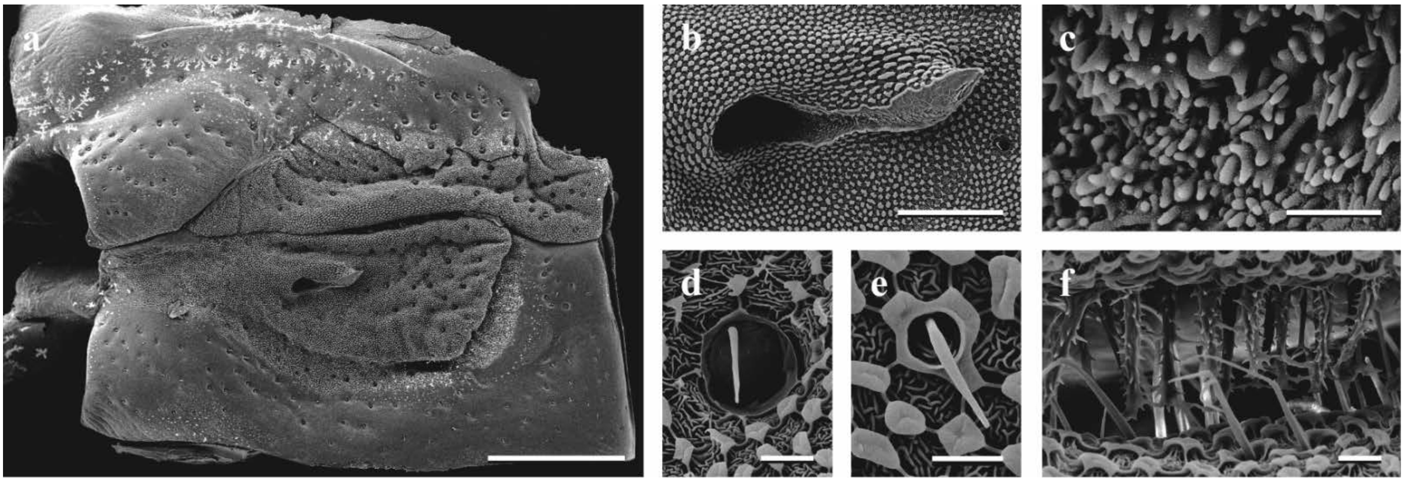

Fig. 8 External scent efferent system of *Coptochilus ferrugineus*. (A) Meso- and metapleuron. (B) Peritreme. (C) Peritremal surface. (d-e) Details of evaporatorium. (f) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c) 5 µm; (d-f) 10 µm

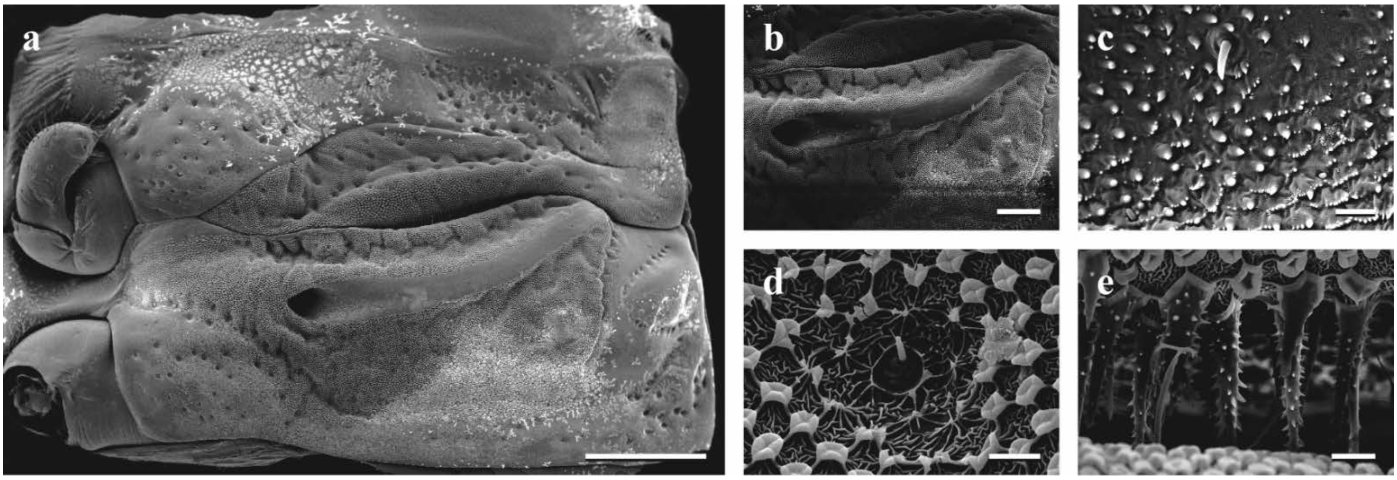

Fig. 9 External scent efferent system of *Crathis ansata*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 10 µm

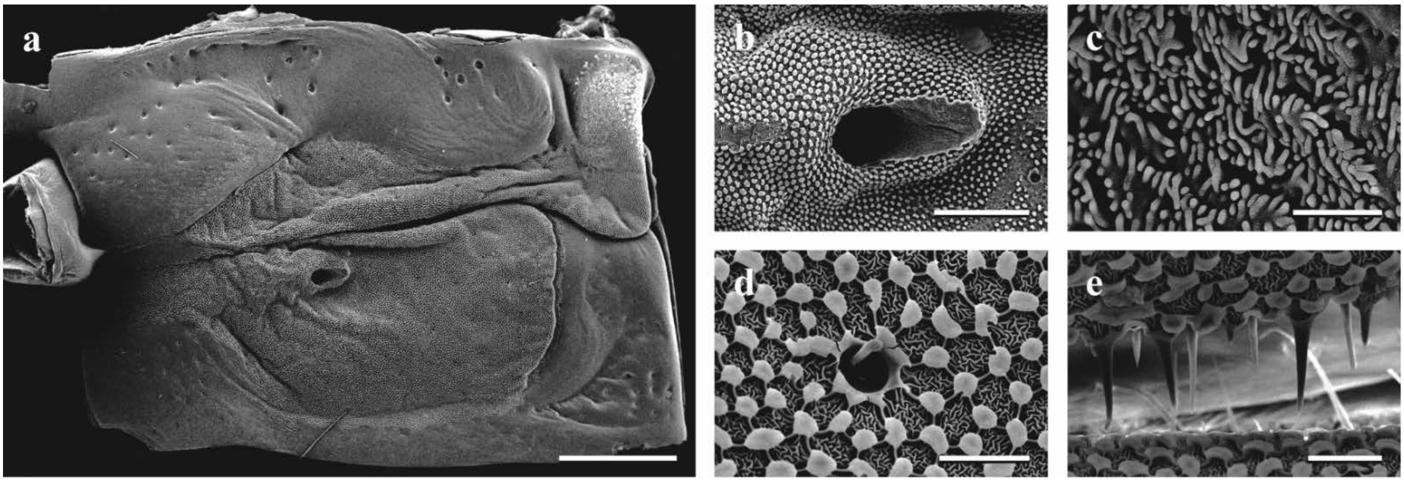

Fig. 10 External scent efferent system of *Diolcus irroratus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c) 5 µm; (d-e) 20 µm

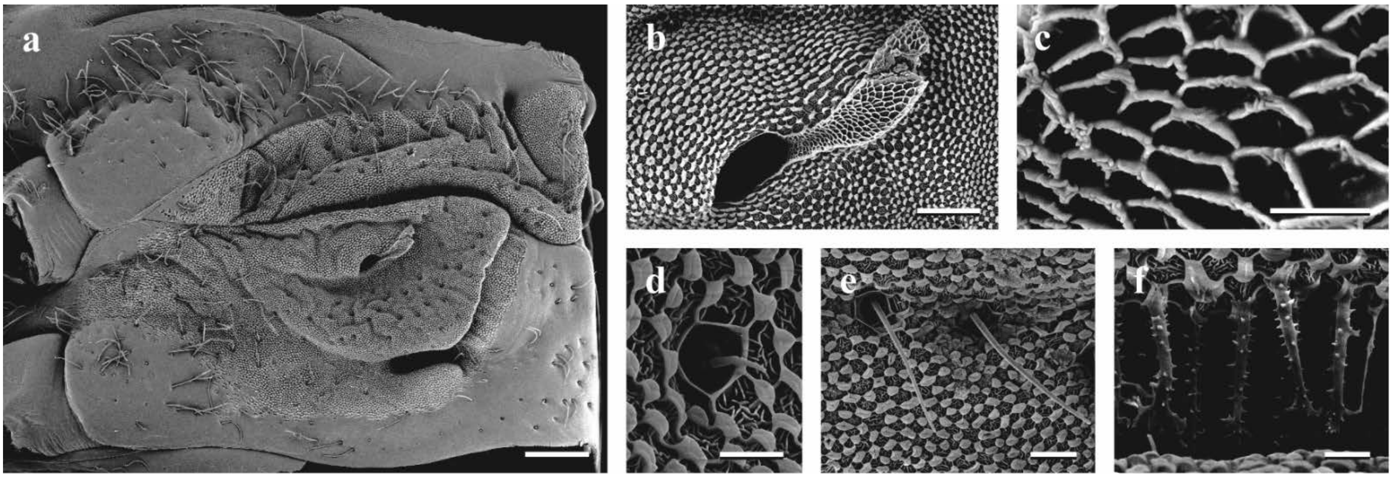

Fig. 11 External scent efferent system of *Dystus puberulus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d-e) Details of evaporatorium. (f) Spiracular filter system. Bars: (a) 200 µm; (b, e) 20 µm; (c, d, f) 10 µm

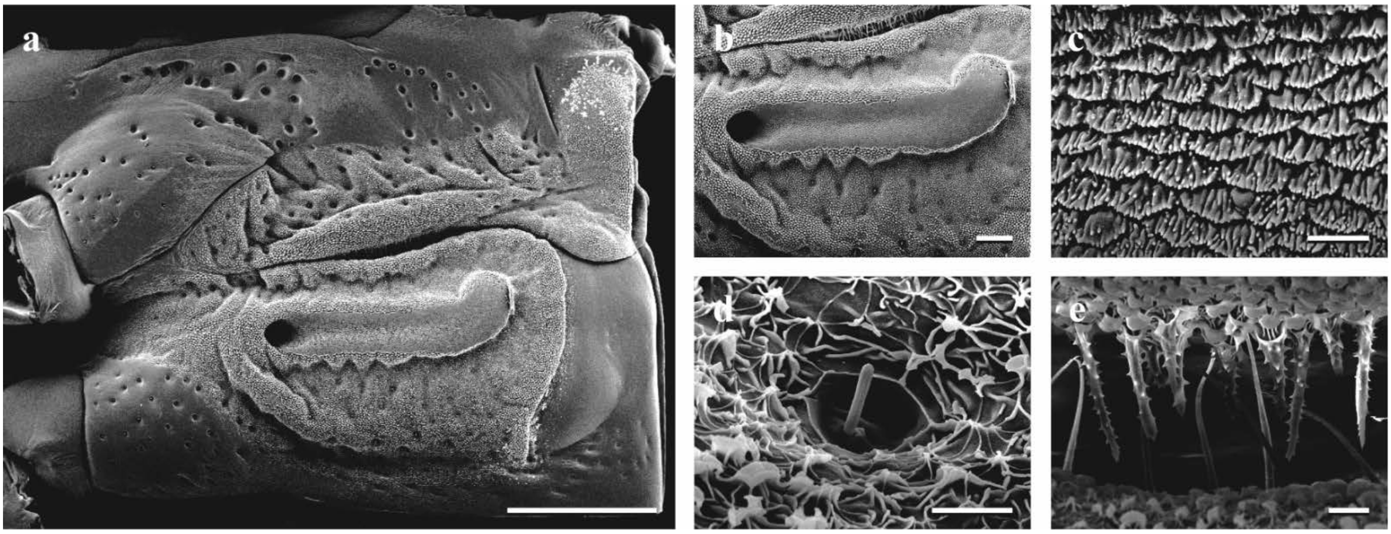

Fig. 12 External scent efferent system of *Galeacius martini*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-e) 10 µm

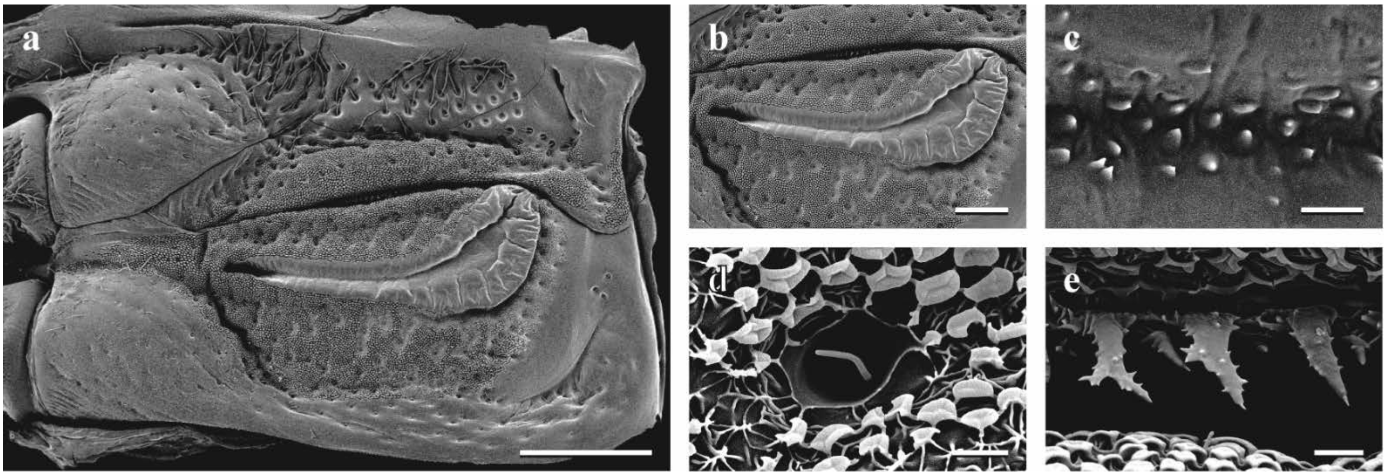

Fig. 13 External scent efferent system of *Homaemus aeneifrons*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 10 µm

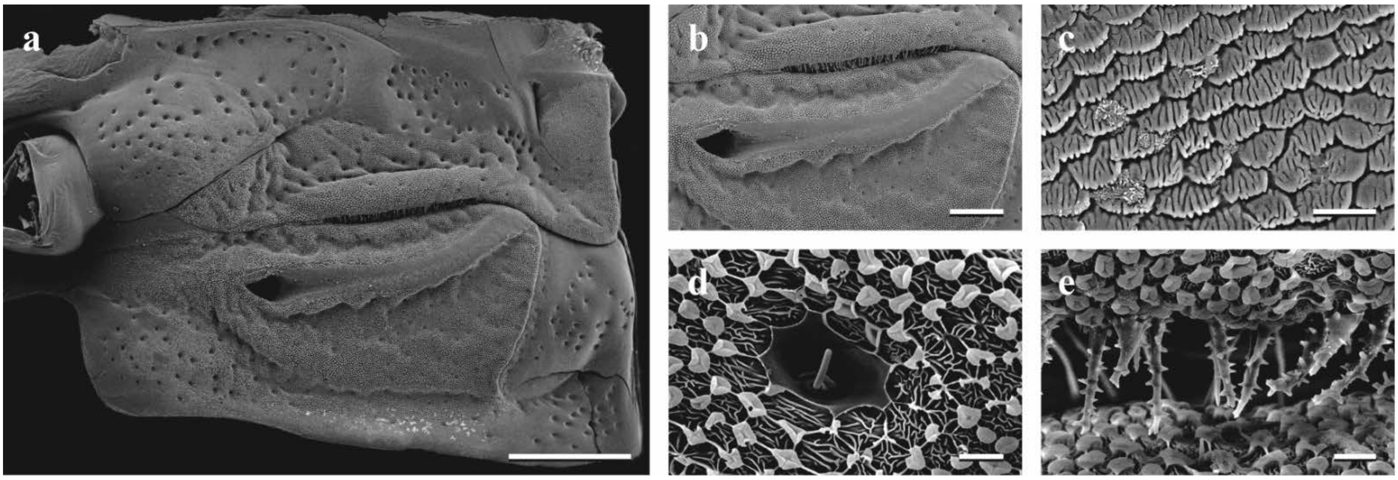

Fig. 14 External scent efferent system of *Lobothyreus lobatus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 10 µm

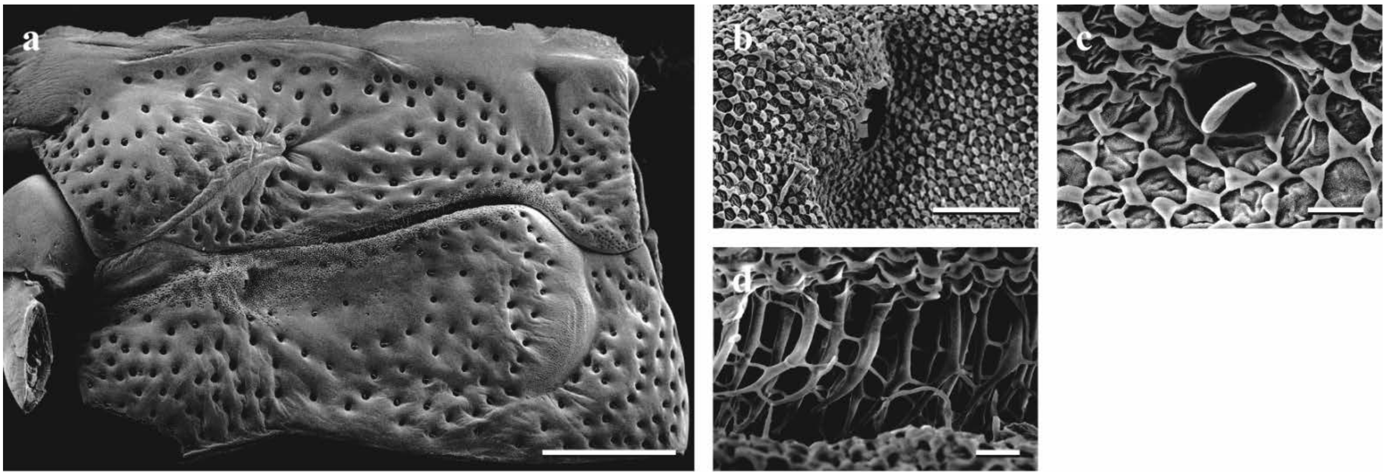

Fig. 15 External scent efferent system of *Misippus spinolae*. (a) Meso- and metapleuron. (b) Peritreme. (c) Detail of evaporatorium. (d) Spiracular filter system. Bars: (a) 500 µm; (b) 50 µm; (c-d) 10 µm

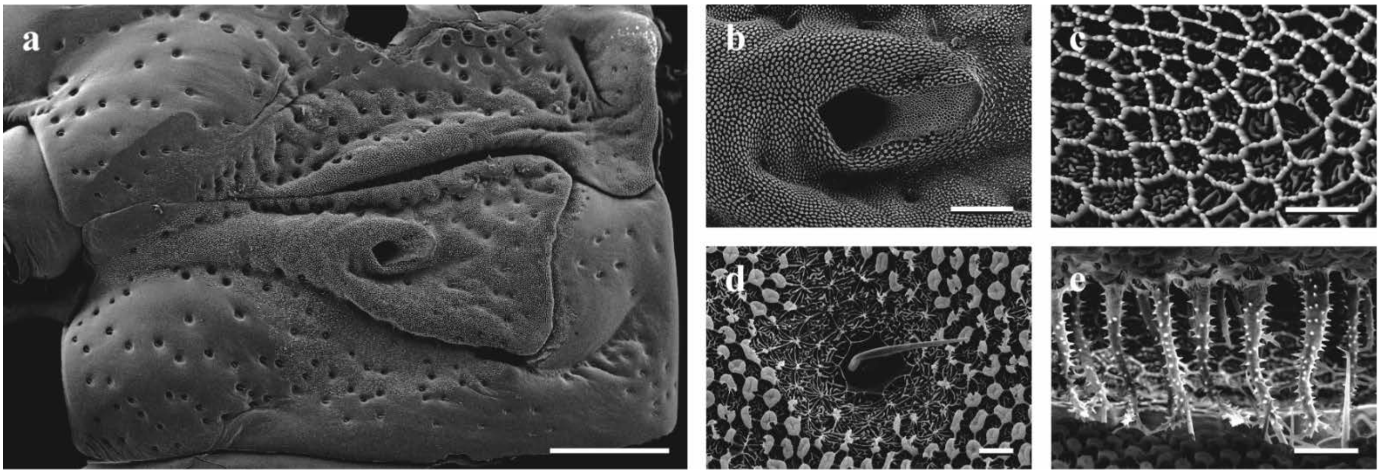

Fig. 16 External scent efferent system of *Orsilochides variabilis*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-d) 10 µm; (e) 20 µm

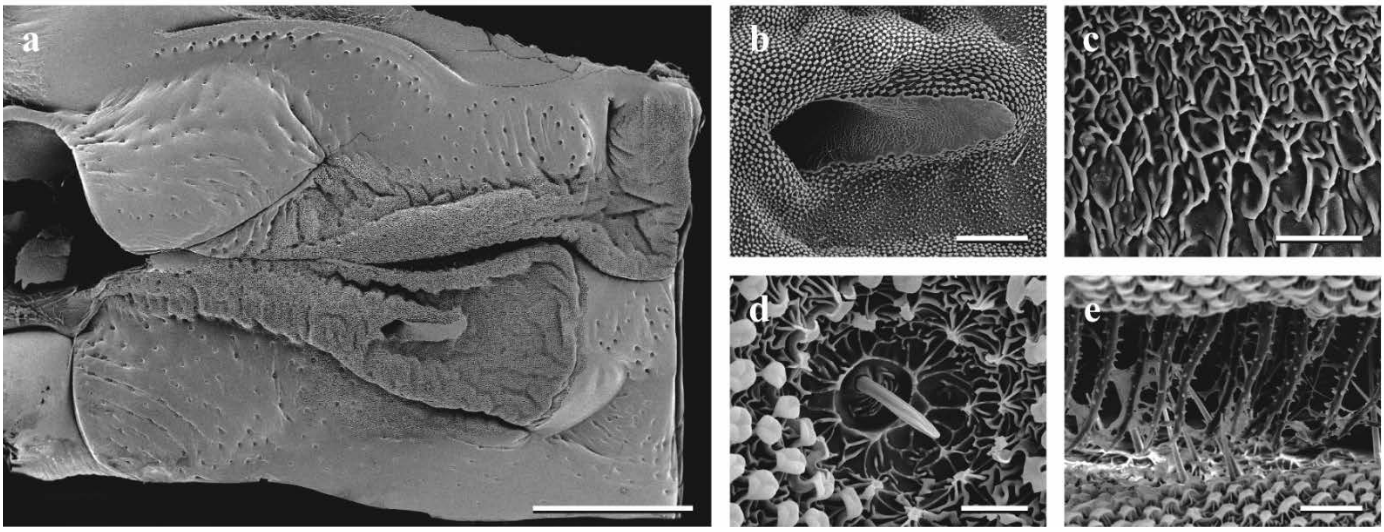

Fig. 17 External scent efferent system of *Pachycoris torridus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 1 mm; (b) 100 µm; (c-d) 10 µm; (e) 20 µm

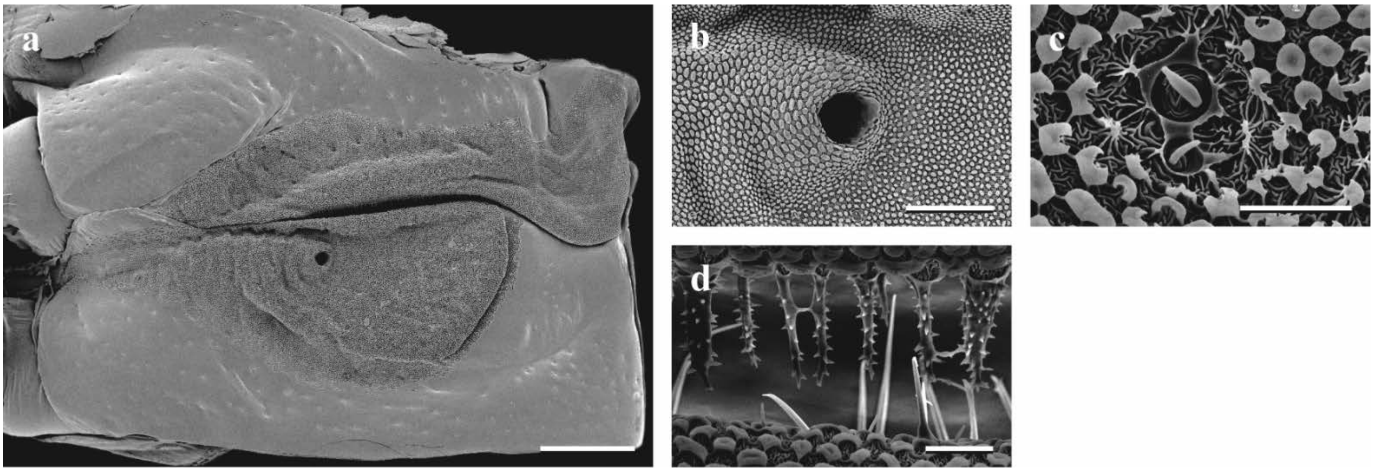

Fig. 18 External scent efferent system of *Polytes lineolatus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Detail of evaporatorium. (d) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-d) 20 µm

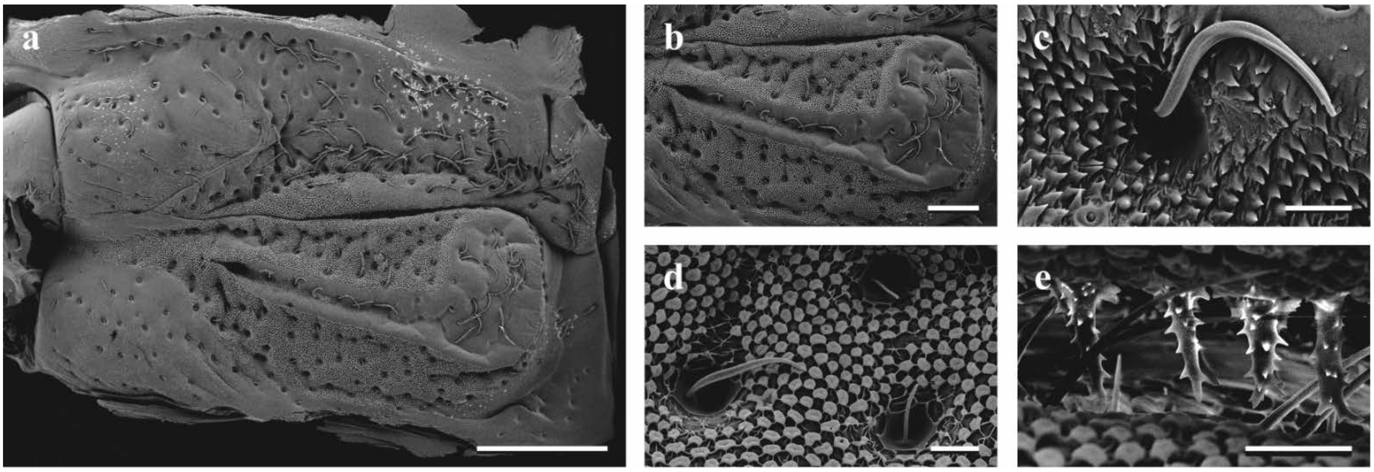

Fig. 19 External scent efferent system of *Sphyrocoris obliquus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 20 µm

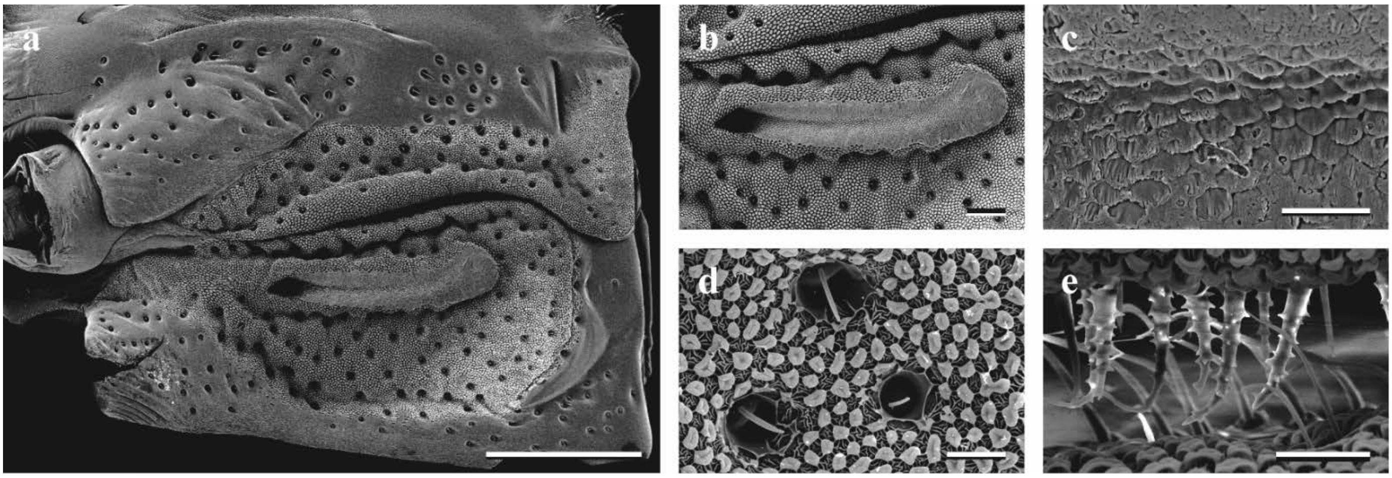

Fig. 20. External scent efferent system of *Stethaulax marmorata*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 20 µm

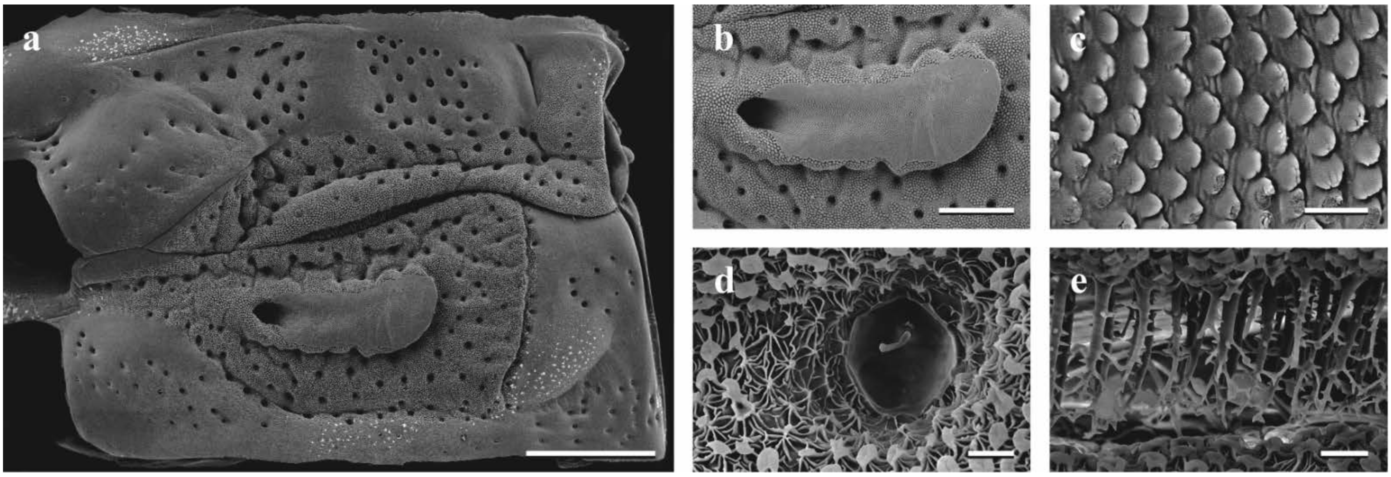

Fig. 21 External scent efferent system of *Symphylus ramivitta*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 200 µm; (c-e) 10 µm

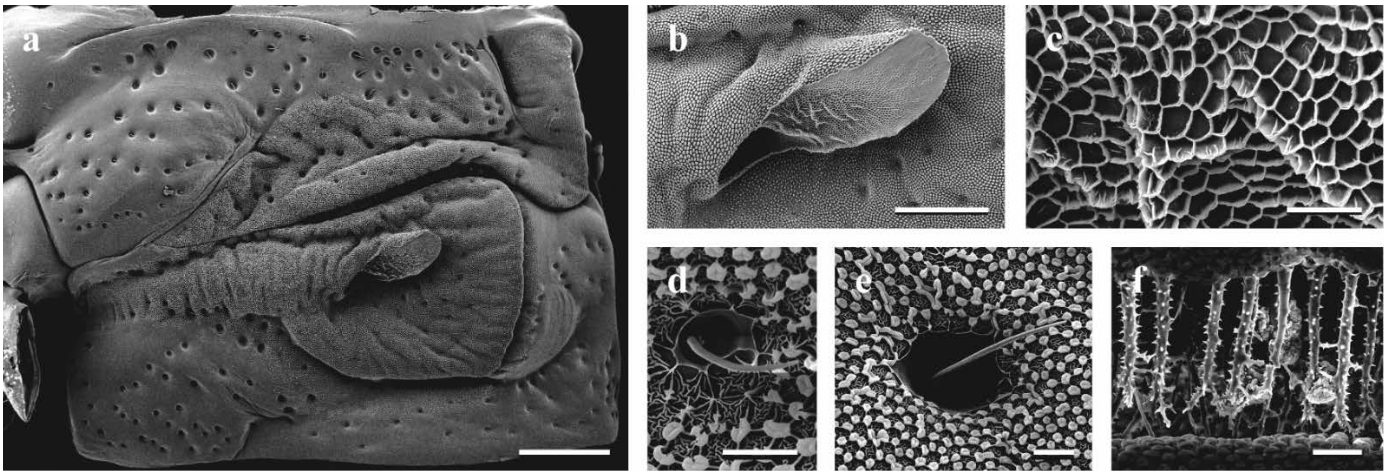

Fig. 22 External scent efferent system of *Tetyra antillarum*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d-e) Details of evaporatorium. (f) Spiracular filter system. Bars: (A) 500 µm; (B) 200 µm; (C-F) 20 µm.

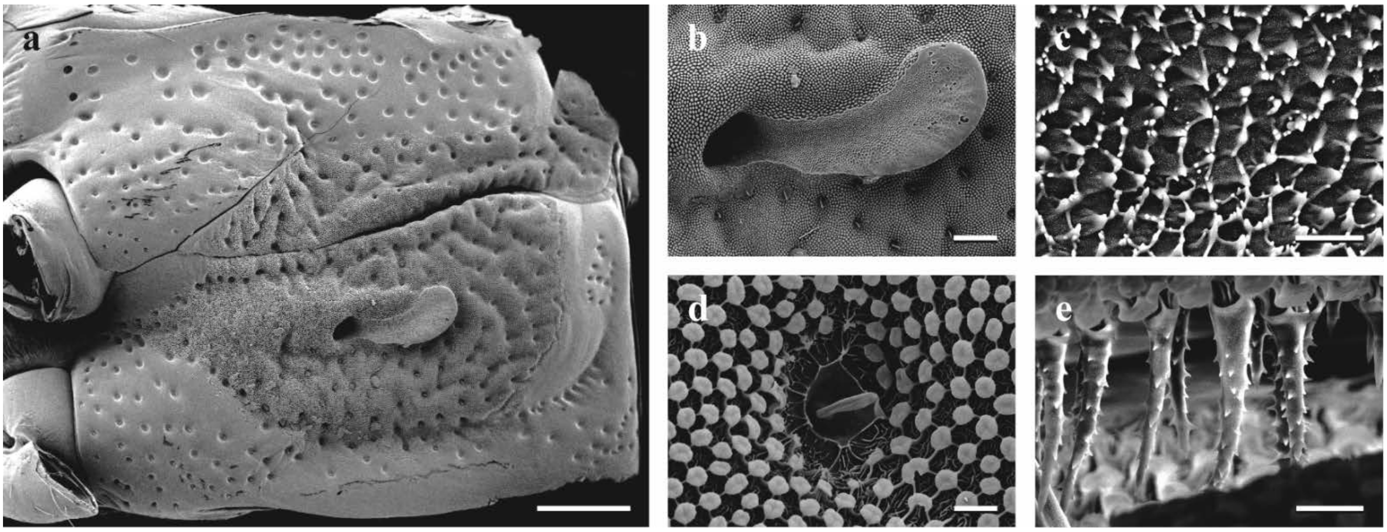

Fig. 23 External scent efferent system of *Tiridates rubrocinctus*. (a) Meso- and metapleuron. (b) Peritreme. (c) Peritremal surface. (d) Detail of evaporatorium. (e) Spiracular filter system. Bars: (a) 500 µm; (b) 100 µm; (c-e) 10 µ

CAPÍTULO II[1]

First Approach of the Pachycorinae Amyot & Serville Phylogeny

(Hemiptera: Heteroptera: Scutelleridae)

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Abstract

Pachycorinae is the largest subfamily within Scutelleridae in the Neotropical region, presenting genera with Nearctic distribution as well. Phylogenetic analyses of 22 of the 24 known genera of the subfamily Pachycorinae based on morphological characters were performed under equal and implied weighting. Species from the remaining seven scutellerid subfamilies Elvisurinae, Eurygastrinae, Hoteinae, Odontoscelinae, Odontotarsinae, Scutellerinae and Tectocorinae were included as outgroups, and the tree rooted on *Augocoris*. Ninety morphological characters were coded in the data matrix. The cladistic analyses did not recover the monophyly of the subfamily Pachycorinae. A clade was supported based on characters of the metathoracic scent apparatus and abdomen, demonstrating the relationship within the majority of species current placed in Pachycorinae.

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[1] Artigo formatado segundo normas do periódico Invertebrate Systematics.

Additional keywords: Neotropical, shield bugs, taxonomy, morphology, cladistics, parsimony, implied weights

Introduction

The Scutelleridae is one of the most speciose families of landbugs within Pentatomoidea comprising about 80 genera and nearly 500 species (Cassis and Vanags 2006; Tsai *et al.* 2011). Distributed in all geographic regions, they are known as shield or jewel bugs and are recognized by the greatly enlarged scutellum, which covers most part or the entire abdomen, leaving the hemelytra minimally exposed. Due to the very bright and iridescent colors some members present, they are among the most spectacularly colored bugs of suborder Heteroptera (Schuh and Slater 1995). Nevertheless, many species are dull in coloration (Eger *et al.* 2015) exhibiting patterns of pale and dark castaneous with apparently cryptozoic habits (Cassis and Vanags 2006).

Surprisingly, in spite of these characteristics and their relatively large size, scutellerids received little attention in the past century (Tsai *et al.* 2011). Scutellerids are consistently maintained as a distinct family (Schuh and Slater 1995; Cassis and Gross 2002; Göllner-Scheiding 2006; Grazia *et al.* 2008), even being defined by a set of characters there are highly homoplasious within Pentatomoidea (Cassis and Vanags 2006; Tsai *et al.* 2011).

The infra-familial classification of Scutelleridae derives from the classical Stål papers (1872; 1873) (Cassis and Vanags 2006), and despite the efforts of many authors (e.g. Leston 1952a; 1952b; 1952c; 1952d; 1954; 1958; McDonald and Cassis 1984; Fischer 2001; Carapezza 2009) it is still uncertain since the phylogenetic relationship among the groups is poorly explored and unclear (Tsai *et al.* 2011). Göllner-Scheiding (2006) established seven subfamilies (Elvisurinae Stål, 1872, Eurygastrinae Amyot & Serville, 1843, Odontoscelinae Amyot & Serville, 1843, Odontotarsinae Mulsant & Rey, 1865, Pachycorinae Amyot & Serville, 1843, Scutellerinae Leach, 1815, and Tectocorinae (McDonald and Cassis, 1984), and Carapezza (2009) defined Hoteinae to separate two African genera from Pachycorinae.

Taxonomic decisions within Scutelleridae have been taken without phylogenetic investigations since the only study that explores the relationships between species of the subfamily is that of Fischer (2001); however, the author includes only 12 of the 26 genera belonging to the subfamily so far, besides not using cladistics methods for the analysis. Carapezza (2009) proposes the new subfamily Hoteinae for the genera *Hotea* Amyot & Serville, 1843 and *Deroplax* Mayr, 1864, originally placed in Pachycorinae, separating them based on male and female internal genitalia structures, besides considering incongruent the geographical distribution of these genera with the other group members (Neotropical and/or Nearctic). However, the author does not use cladistics or biogeographic methods to support these arguments.

Pachycorinae is the largest subfamily in the Neotropical region, including also seven genera with distribution throughout the American continent and one genus with exclusively Nearctic distribution (Schuh and Slater 1995; Eger *et al.* 2015). Pachycorinae members range in length 5 to 20mm and are quite diverse in coloration, presenting presumably cryptozoic and aposematic colors. Generally considered to be exclusively phytophagous, the fact that they are not reported as monoculture big pests contribute for the little attention that they have been received (Eger *et al.* 20015). Currently with 24 genera and 115 species, several species of the subfamily present polymorphism and sexual dimorphism, what have caused many misunderstood descriptions and nomenclatural confusion as well (Eger *et al.* 2015). Therefore, the species number is probably misestimated once some genera urgently need revision. Merely for *Tiridates* Stål, 1867 (Eger 1987), *Polytes* Stål, 1867 (Eger 1990), *Agonosoma* Laporte, 1832 (Paleari 1992) and *Sphyrocoris* Mayr, 1864 (Eger 2012) there are recent taxonomic revisions. *Crathis* Stål, 1861, *Lobothyreus* Mayr, 1864 and *Tetyra* Fabricius, 1803 are now under review (Barcellos, in prep.).

The pachycorines are historically characterized by exhibiting 1 + 1 stridulatory areas on the abdomen associated with a tibial plectrum and by presenting a single intervannal vein in the hind wing (Schouteden 1904; Lattin 1964; Fischer 2001; Cassis and Vanags 2006; Tsai *et al.* 2011; Eger *et al.* 2015). However, both features seemed to have evolved more than once within Scutelleridae and some authors questioned the monophyly of the subfamily based on these characters (e.g. Lattin 1964; Carapezza 2009; Tsai *et al.* 2011). Cassis and Vanags (2006) reported to have found stridulatory vittae on *Nesogenes* Horváth, 1921 and *Vanduzeenia* Schouteden, 1904 and Carapezza (2009) atested that *Ellipsocoris* Mayr, 1864 also possesses the structures. Carapezza (2009) excluded *Hotea* and *Deroplax*, previously placed on Pachycorinae, both presenting stridulatory areas. Furthermore, according to Tsai *et al.* (2011), the subfamily is very diverse in several aspects, besides not presents uniform patterns of both male and female genitalia, what would make its monophyly doubtful.

In this study, the position of Pachycorinae among Scutelleridae and the relationships amongst the species of the subfamily are evaluated for the first time through cladistic methodology, based on morphological characters. The results presented here supply valuable information about the morphology of this poorly known group of species as well as their relationship among scutellerid subfamilies and the relation within its genera.

Methods

Taxon sampling

A total of 66 taxa were included in the matrix (Table 1): 50 species belonging to 22 of the 24 known genera of Pachycorinae as ingroup and 16 species as outgroup belonging to the remaining seven subfamilies of Scutelleridae, as follow: Scutellerinae – *Augocoris gomesii* Burmeister, 1835, *Chrysocoris purpureus* (Westwood 1837), *Sphaerocoris testudogrisea* (de Geer 1778); Elvisurinae – *Coleotichus costatus* (Fabricius, 1787), *Solenosthedium liligerum* (Thunberg, 1783); Eurygastrinae – *Eurygaster alternata* Say 1828), *Eurygaster integriceps* Puton 1881; Odontotarsinae – *Vanduzeenia balli* (Van Duzee, 1904), *Euptychodera corrugata* (Van Duzee, 1904); Odontoscelinae – *Odontoscelis fuliginosa* (Linnaeus, 1761), *Irochrotus maculiventris* (Germar, 1839); Hoteinae – *Hotea curculionoides* (Herrich-Schäffer 1836), *Hotea subfasciata* (Westwood, 1837), *Deroplax silphoides* (Thunberg, 1783), *Deroplax nigrofasciata* Distant, 1898; Tectocorinae – *Tectocoris diophthalmus* (Thunberg, 1783).

The cladogram was rooted on *Augocoris gomesii*, once it is the only representative Neotropical species besides Pachycorinae. Furthermore, Scutellerinae is recognized mostly by the lack of apomorphies that define the other subfamilies (Tsai *et al.* 2011), being interesting for character polarization.

The following species were used as ingroup: *Agonosoma flavolineata* Laporte, 1832; *Acantholomidea denticulata* (Stål, 1870); *Acantholomidea porosa* (Germar, 1839); *Agonosoma trilineatum* Laporte, 1832; *Ascanius hirtipes* (Herrich-Schäffer, 1836); *Camirus moestus* (Stål, 1862); *Chelycoris haglundi* (Montandon, 1895);

Chelycoris lethierryi (Montandon, 1895); *Chelyschema trinotata* (Walker, 1867); *Coptochilus ferrugineus* Amyot & Serville, 1843; *Coptochilus lentiginosus* Berg, 1879; *Crathis ansata* (Distant, 1889); *Crathis longifrons* Stål, 1861; *Diolcus chrysorrhoeus* (Fabricius, 1803); *Diolcus irroratus* (Fabricius, 1775); *Diolcus variegatus* (Herrich-Schäffer, 1836); *Dystus puberulus* Stål, 1862; *Galeacius martini* Schouteden, 1904; *Homaemus aeneifrons* (Say, 1824); *Homaemus parvulus* (Germar, 1839); *Homaemus proteus* Stål, 1862; *Lobothyreus lobatus* (Westwood, 1837); *Misippus spinolae* (Signoret, 1863); *Orsilochides guttata* (Herrich-Schäffer, 1839); *Orsilochides leucoptera* (Germar, 1839); *Orsilochides variabilis* (Herrich-Schäffer, 1837); *Pachycoris fabricii* (Linnaeus, 1771); *Pachycoris klugii* Burmeister 1835; *Pachycoris torridus* (Scopoli, 1772); *Polytes bimaculatus* Eger, 1990; *Polytes confusus* Eger, 1990; *Polytes fenestra* Breddin, 1903; *Polytes granulatus* (Walker, 1868); *Polytes lattini* Eger, 1990; *Polytes leopardinus* Distant, 1911; *Polytes lineolatus* (Dallas, 1851); *Polytes obscurus* (Dallas, 1851); *Polytes ruth* (Breddin, 1903); *Polytes similis* Eger, 1990; *Polytes tigrinus* (Vollenhoven, 1868); *Polytes velutinus* (Dallas, 1851); *Symphylus caribbeanus* Kirkaldy, 1909; *Symphylus cyphonoides* (Walker, 1867); *Symphylus ramivitta* Walker, 1838; *Sphyrocoris obliquus* (Germar, 1839); *Stethaulax marmorata* (Say, 1831); *Tetyra antillarum* Kirkaldy, 1909; *Tetyra bipunctata* (Herrich-Schäffer, 1839); *Tiridates mexicanus* (Herrich-Schäffer, 1837); *Tiridates rubrocinctus* (Herrich-Schäffer, 1837).

The genera *Ephynes* and *Testrina* were not included on the matrix, once we have not access to the types and their original descriptions and pictures were not enough detailed to coded characters. The chosen species of *Polytes* are representatives from *Polytes fenestra group* (*P. confusus, P. fenestra, P. lattini, P. leopardinus, P. similis, P.*

ruth) and *Polytes tigrinus group* (*P. bimaculatus*, *P. granulatus*, *P. lineolatus*, *P. obscurus*, *P. tigrinus*, *P. velutinus*) (sensu Eger 1990).

Depositories and abbreviations

The specimens used in this study were borrowed from the following institutions: DARC, David A. Rider Collection, North Dakota State University, North Dakota, United States of America; DZUP, Museu de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Paraná, Brazil; JEEC, Joseph Eger Collection, Dow AgroSciences, Florida, United States of America; MCNZ, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Rio Grande do Sul, Brazil; MGAP, Museu Anchieta, Rio Grande do Sul, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; UFRG, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Rio Grande do Sul, Brazil; USNM, National Museum of Natural History, Washington D.C. United States of America.

Specimen preparation

All material consisted of dried specimens. The genitalia were dissected after short heating in hypertonic potassium hydroxide solution (KOH) and stained with Congo red then examined by Leica MZ 12.5 stereomicroscope. Images were taken with Nikon AZ 100M digital camera and software NIS-Elements software. Genitalia were preserved in glycerin and pinned with the specimen.

Characters and coding

The data matrix (Table 1) was constructed using WinClada (Nixon 2002) and character polarization was achieved using outgroup comparison (Nixon and Carpenter 1993). All characters were treated as discrete. Of the 90 morphological coded characters, 3 are of general morphology, 13 are of head, 38 of thorax, 15 of abdomen, and 21 of female genitalia. Sixty characters were binary and 30 multistate which were treated as non-additive (Fitch 1971).

Some of the characters we analyzed were based on those of Gapud (1991); Hasan and Kitching (1993); Grazia (1997); Henry (1997); Kocorek and Lis (2000); Barcellos and Grazia (2003); Fortes and Grazia (2005); Campos and Grazia (2006); Grazia *et al.* (2008); Bernardes *et al.* (2009); Ferrari *et al.* (2010); Kment and Vilímová (2010); Greve *et al.* (2013); Barão (2015) and Weiler *et al.* 2016. The remaining characters are novelties. The list of characters is provided in Results section. Terminology follows Tsai *et al.* (2011) for general morphology, Kment and Vilímová (2010) for external scent efferent system (ESES) and McDonald (1966), McDonald and Cassis (1984) and Cassis and Vanags (2006) for genital morphology.

The character coding method was the contingent coding (Brazeau 2011); the character statements were elaborated following Sereno (2007). Inapplicable data were coded as "-" and missing data were coded as "?". The following notations for characters are used in Results and Discussion sections: "X(Y)", in which X represents the character and Y represents the state; "s", to the number of steps; "CI", to consistency index (Kluge and Farris 1969); and "RI", to retention index (Farris 1989). Characters that did not support any relationship are indicated as "uninformative", but we chose to keep them in the matrix due to the adoption of contingent coding (Brazeau 2011).

Phylogenetic analyses

Phylogenetic analyses were performed by parsimony with TNT 1.5 (Goloboff and Catalano 2016). The matrix was analyzed under equal weights (EW) and implied weights (IW) (Farris 1989; Goloboff 1993) aiming to find the most stable trees downweighting characters according to their degree of homoplasy (the higher their homoplasy, the lower their weight). In order to explore how the homoplasies would affect relationships among species according to the penalties it receives, we realized three different searches, under K = 3, K = 6 and K = 15.

Analyses were carry out using heuristic searches under 1000 random addition sequences, TBR branch swapping algorithm retaining 50 trees per replication, random seed 3, and holding up to 200,000 trees in memory (rseed 3; mult 1000 = tbr hold 50).

Results

Characters

General characters. Character 0. Vestiture: (0) completely glabrous; (1) setose only ventrally; (2) setose both dorsum and venter.

Character 1. Vestiture, setae, position: (0) setae erected (1) not erected.

Character 2. Vestiture, not erected setae, structure: (0) curly; (1) straight.

Character 3. Head. Head, shape: (0) triangular; (1) quadrangular.

Character 4. Clypeus, length related to apex of jugae: (0) longer; (1) subequal; (2) shorter.

Character 5. Head, dorsum, curvature: (0) plane, not curved; (1) strongly convex; (2) convex rounded.

Character 6. Head, length in relation to width (between the eyes): (0) longer than wide; (1) wider than long; (2) approximately the same.

Character 7. Jugae, lateral margins, shape: (0) carinate; (1) rounded.

Character 8. Gena, genal suture, shape: (0) carinate; (1) flat.

Character 9. Clypeus, apex, shape: (0) rhombus; (1) rounded.

Character 10. Jugae, level in relation to clypeus' level: (0) same; (1) above; (2) below.

Character 11. Maxilary plates, anterior region, length in relation to mandibular plates: (0) almost the same; (1) longer, but not touching in front of clypeus; (2) shorter; (3) longer, touching in front of clypeus.

Character 12. Bucculae, anterior lobe, shape: (0) weakly sinuate; (1) greatly explanate.

Character 13. Labium, length related to metacoxae and abdominal segment III (SIII): (0) very long, surpassing SIII; (1) short, not surpassing metacoxae; (2) moderately long, surpassing metacoxae but not SIII.

Character 14. Labium, length of LI related to bucculae: (0) surpassing; (1) not surpassing, contained in between.

Character 15. Eyes, shape: (0) semicircular or rounded; (1) elliptical.

Character 16. *Thorax.* Pronotum, anterolateral margins, shape: (0) entirely carinate; (1) entirely rounded; (2) rounded anteriorly, carinate at humeral angles.

Character 17. Pronotum, humeral angles, form: (0) not projected, almost in line with hemelytra; (1) projected.

Character 18. Pronotum, humeral angles, shape: (0) entire, continuous; (1) interrupted, discontinuous.

Character 19. Pronotum, external transverse suture: (0) absent, pronotum uniform; (1) present, pronotum divided.

Character 20. Pronotum, anterolateral angles, shape: (0) with a small anterolaterad projection; (1) not projected.

Character 21. Scutellum, external transverse suture: (0) absent; (1) present.

Character 22. Scutellum, width related to connexiva: (0) very large, covering connexiva; (1) narrower, not covering connexiva.

Character 23. Scutellum, length related to end of abdomen: (0) surpassing; (1) not surpassing.

Character 24. Scutellum, posterolateral margin: (0) simple; (1) raised in a flap.

Character 25. Scutellum, fovea: (0) present; (1) absent.

Character 26. Scutellum, fovea, width related to width of an eye: (0) wider; (1) subequal.

Character 27. Scutellum, fovea, depth: (0) shallow; (1) deep.

Character 28. Scutellum, callus inner region fovea: (0) absent; (1) present.

Character 29. Proepisternum, keel (Pe(K)), explanation related to annteniferous tubercle: (0) touching, not surpassing the tubercle; (1) surpassing, covering the tubercle.

Character 30. Proepisternum, Pe(K), anterior margin, shape: (0) rounded; (1) sinuate; (2) rectilinear.

Character 31. Mesosternum, lateral margins, keel (Me(K)): (0) absent; (1) present.

Character 32. Mesosternum, Me(K), height in relation to body plan: (0) barely elevated; (1) extremely elevated, contiguous with Pe(K); (2) moderatly elevated.

Character 33. Metasternum, keel: (0) absent; (1) present.

Character 34. Meso- and metasternum, medial groove, depth: (0) shallow; (1) deep.

Character 35. External scent efferent system (ESES): (0) present; (1) absent, obsolete.

Character 36. ESES, peritreme: (0) present; (1) absent.

Character 37. ESES, peritreme, shape: (0) groove; (1) ruga; (2) spout; (3) auricle.

Character 38. ESES, peritremal groove, form: (0) distinctly elevated in one region; (1) flat, not elevated; (2) whole structure distinctly elevated equally.

Character 39. ESES, peritreme spout, form: (0) developed; (1) rudiment.

Character 40. ESES, ostiole opening, orientation: (0) ventrolaterally; (1) posterolaterally; (2) ventrally; (3) laterally.

Character 41. ESES, ostiole, shape: (0) guttiform; (1) round; (2) slit-like; (3) elliptical.

Character 42. ESES, periostiolar depression: (0) present; (1) absent.

Character 43. ESES, ostiole, position related to metapleuron and coxae: (0) closer to metacoxal cavity; (1) medially on metapleuron.

Character 44. ESES, evaporatorium, occupation area: (0) enlarged, well developed on meso- and metapleuron; (1) reduced, poorly developed on meso- and metapleuron; (2) well developed on metapleuron, poorly developed on mesepimeron.

Character 45. ESES, evaporatorium, punctures: (0) absent; (1) present.

Character 46. Metathoracic spiracle, form: (0) wide; (1) narrow.

Character 47. Metapleuron, lateral margin of ostiolar plate: (0) evanescent; (1) elevated.

Character 48. ESES, outer margin of evaporatorium, shape: (0) convex; (1) concave; (2) sigmoid; (3) straight.

Character 49. ESES, metepimeral pseudosuture: (0) depressed; (1) not depressed, same level of ostiolar plate.

Character 50. ESES, depressed metepimeral pseudosuture, region of depression: (0) all along extension equally; (1) deeply depressed all along extension + deeply at posterolateral region.

Character 51. Hind wing, posterior cubital vein (CuP) (glochis (gCu) *sensu* Tsai *et al.* 2011): (0) absent; (1) present.

Character 52. Hind wing, intervannal vein (Iv): (0) present; (1) absent.

Character 53. Hind wing, Iv, shape: (0) V-shaped; (1) Y-shaped; (2) single branched.

Abdomen. Character 54. Androconial glands: (0) absent; (1) present.

Character 55. Abdominal lateral margins, shape: (0) rounded; (1) carinate.

Character 56. Urosternites, poterolateral angles, form: (0) not projected; (1) projected.

Character 57. Urosternites, projected posterolateral angles, shape: (0) rounded, tubercle; (1) into spines.

Character 58. Urosternites IV, V and VI, form: (0) semicircular; (1) trapezoid.

Character 59. Urosternites, spiracles, adjacent area, callus: (0) absent; (1) present.

Character 60. Connexivum, coloration pattern: (0) unicolor; (1) bi-color.

Character 61. Urosternites, spiracles, color in relation to the color of adjacent area: (0) concolour; (1) not-concolour.

Character 62. Urosternites, anterolateral angles, form: (0) not projected; (1) projected, callous.

Character 63. Urosternites lateral margin, orientation: (0) shifted upwards; (1) regular, viewed laterally.

Character 64. Abdominal sternite VII (SVII) in males, length related to genital segments: (0) short, regular, not covering genitalia; (1) long, covering genitalia.

Character 65. SVII in females, posterior margin, shape: (0) straight; (1) with one projection medially; (1) with two projections.

Character 66. Abdomen, lateral border, shape: (0) laterad convex; (1) laterad compressed.

Character 67. Stridulatory area: (0) absent; (1) present.

Character 68. Stridulatory area, extension: (0) SV-SVI; (1) SIV-SVI; (2) SIV-VII; (3) SV-SVII.

Female genitalia. Character 69. Genital segments, orientation related to body plan: (0) caudal; (1) ventral.

Character 70. Genital plates, second gonocoxae (2Gx.) in relation to first gonocoxae (1Gx.): (0) exposed; (1) covered.

Character 71. Genital plates, paratergites VIII (Pt.8), spiracles: (0) present; (1) absent.

Character 72. Genital plates, paratergites XI (Pt.9), lateral border, length in relation to SVII: (0) not reaching margin of SVII (very short); (1) almost reaching margin of SVII (long); (2) touching margin of SVII (very long).

Character 73. Tergite VIII, posterior border, orientation in relation to body plan: (0) parallel; (1) perpendicular, strongly declivous posteriorly; (2) slightly declivous posteriorly.

Character 74. Genital plates, 1Gx and Pt.9, orientation in relation to body plan: (0) parallel; (1) perpendicular.

Character 75. Genital plates, Pt.9, inner margins: (0) separated; (1) juxtaposed; (2) overlapping.

Character 76. Genital plates, Pt.8, inner margins: (0) separated; (1) juxtaposed.

Character 77. Genital plates, anterior margin of Pt.9 in relation to 1Gx.: (0) juxtaposed; (1) above; (2) beneath.

Character 78. Genital plates, segment X in relation to Pt.9: (0) exposed; (1) covered.

Character 79. Genital plates, posterior margin of 1Gx., shape: (0) sinuous; (1) rectilinear; (2) concave; (3) convex.

Character 80. Genital plates, rectilinear posterior margin of 1Gx., orientation: (0) transversal; (1) oblique upward; (2) oblique downward.

Character 81. Genital plates, 1Gx., sutural margins: (0) juxtaposed basally, divergent apically; (1) juxtaposed along all extension; (2) separated; (3) juxtaposed medially; (4) overlapping.

Character 82. Genital plates, Pt.9, sutural margins, shape: (0) simple; (1) emarginate.

Character 83. Genital plates, 1Gx., sutural margins, shape: (0) simple; (1) emarginate.

Character 84. Genital plates, Pt.9, orientation in relation to 1Gx.: (0) co-planar; (1) bi-planar, obtusely oriented.

Character 85. Ectodermal genital tracts, spermathecal dilation: (0) present; (1) absent.

Character 86. Ectodermal genital tracts, spermathecal dilation, form: (0) spherical; (1) elliptical; (2) tubular; (3) bean-shaped.

Character 87. Ectodermal genital tracts, spermathecal bulb, form: (0) clavate short; (1) saccular short; (2) oval/globose/oblong; (3) clavate long; (4) saccular long.

Character 88. Ectodermal genital tracts, spermathecal dilation, location in relation to spermathecal duct: (0) contiguous; (1) lateral.

Character 89. Ectodermal genital tracts, spermathecal dilation, degree of sclerotization: (0) highly sclerotized; (1) poorly sclerotized, membranous; (2) slightly sclerotized.

Cladistic analysis

The analysis under EW resulted in 76 trees with 567 steps and the consensus of those trees are shown on Fig. 1, CI = 0.22 and RI = 0.62. The analyses using IW under different K-values resulted in one tree each search, with distinct topologies: K = 3 one tree with 585 steps (Fig. 2); K = 6 one with 577 steps (Fig. 3) and when K = 15, another one with 569 steps (Fig. 4).

Discussion

The results of our analyses found that Pachycorinae is a paraphyletic group, due to the placement of Hoteinae, Odontoscelinae and Odontotarsinae subfamilies within the ingroup species. However, a clade (C) was recovered as monophyletic in all the IW analysis and, even though the consensus of EW analysis shows unresolved relationships between Pachycorinae genera, is possible to recognize the same grouping on this topology. The clade C is composed of 43 species of the 50 Pachycorinae species included in our data matrix in two topologies (K = 6 and K = 15) and the species *Misippus spinolae* floats between outgroup clades in EW consensus and K = 3 topologies, very likely to the separated paratergites VIII [76(0)].

The remaining seven ingroup species appear grouped in an also consistent clade (B), closely related to all Hoteinae, Odontoscelinae and Odontotarsinae species analyzed. This clade is supported by characters of vestiture ([0(2)], [1(1)]), the remarkable convexity of the head ([5(1)], [5(2)]), abdomen [57(0)] and ESES characteristics, such as the occupied area by the stridulitum [68(0)] and the evaporatorium ([42(1)], [44(2)]) besides the caudal orientation of the female genital plates [69(0)]. All these characters are, yet, very homoplasious.

The clade C seems to be robust and its support is due to three characters of metathoracic apparatus (wide spiracle [46(0)], elevated lateral margin of ostiolar plate [47(1)], depressed metepimeral pseudosuture [49(0)]) and the absence of projection on urosternites posterolateral angles ([56(0)] with several taxa reversions).

Pachycorinae is primarily characterized by presenting stridulatory areas on the abdominal sterna associated with a tibial plectrum and also by the presence of a single intervannal vein in the hind wing (Fischer 2001; Tsai *et al.* 2011; Eger *et al.* 2015). Nevertheless, our analysis showed what it was already observed by other authors (e.g. Lattin 1964; Cassis and Vanags 2006; Carapezza 2009; Tsai *et al.* 2011) that the stridulitum and the tibial tubercles are not an exclusive characteristic of the pachycorines, occurring in both *Hotea* and *Deroplax* genera as well [67(1)]. Cassis and Vanags (2006) mentioned that *Vanduzeenia* presents the structure, but that observation could be possible a misidentified bug (Cassis, pers. comum.). The single branched intervannal vein is actually a characteristic observed [53(2)] in 48 species of the 50 Pachycorinae studied species (absent in *Acantholomidea denticulata* and *Acantholomidea porosa* [52(1)]), but it also occurs in *Tectocoris diophthalmus* and *Eurygaster integriceps*. The absence of the intervannal vein observed in both *Acantholomidea* species is shared with *Euptychodera corrugata* and *Irochrotus maculiventris,* as is was pointed out for Czaja (2007).

Carapezza (2009) removed *Hotea* and *Deroplax* from Pachycorinae and created them a new subfamily based on the unique male and female internal genitalia. Tsai *et al.*

(2011) argue that the pachycorines are quite diverse in many characteristics beyond their discrepant and disuniform patterns of both male and female genitalia, leading its monophyly doubtful and unlikely. Our data shows that it seems to be true, since all characters that occur in Pachycorinae are highly homoplasious. A large number of missing data of female genitalia on the matrix leads to unsolved relationships, especially within *Polytes* species, that are quite rare on the field and on entomological collections (Eger, 1990). The species of *P. fenestra* and *P. tigrinus* group appear much merged among themselves, demonstrating that these groups are not stable and uniform.

Once characters of the genital capsule and of the phallus are largely known to be indispensable to distinguish between taxa at several taxonomical ranks (Cassis and Vanags 2006), it is hard to test or recover the monophyly of Pachycorinae without male genitalia. Even though the other subfamilies seems to be as well weakly supported for few highly homoplasious characters or for the lack of synapomorphies/ apomorphies, the general characters evidence not be enough for recover groups with robustness, being essential the exploration and study of genital capsule and phallus as well. It is clearly seen by the close relationships observed on clade C, especially among Odontoscelinae and Odontotarsinae within Pachycorinae genera.

All Pachycorinae genera which we have included more than one species were recovered monophyletic. Although the monophyly of the subfamily was not supported, relations that are frequently recovered on different topologies, under different searches parameters (EW, IW when K = 3, K = 6 and K = 15) demonstrate the existence of a monophyletic group formed by 17 genera of the 22 pachycorines studied here (clade C).

The results show the relationships among outgroup species is tenuous and not strongly defined, once taxa are floating among themselves, demonstrating the need of not just the exploration of more characters (male genitalia) but the inclusion of more representative species of all scutellerid subfamilies.

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Table 1. Character state matrix for the cladistic analyses of Pachycorinae

	0 5 10 15 20 25 30 35 40 45 50 55 60	65 70 75 80
Augocoris gomesii	0--00000000000000000000000000000-000000-00000000000000000-0-0	0000000-00000000000-000000000
Chrysocoris purpureus	0--000010100000001011100001000010000000-0000000011-10000110-0	0000100-00101100001010110110-
Sphaerocoris testudogrisea	0--01010100100010010100001---0010000011-00000000200101010-0-1	0010010-011101110110100000000
Coleotichus unicolor	0--00021110001101100101001---1011110000-1000000000000011110-0	0010110-10000111010-200000000
Solenosthedium liligerum	10-00000010001000000000001---101111002-0010000001000101111000	0010110-100101110110300000?00
Eurygaster alternata	0--010211112010001001010000001110010001-2210011001-00?010-101	1010010-10010111000-100012001
Eurygaster integriceps	0--01011111201-000011010000011110110002-2210011101-002010-101	1010010-100101111010100001001
Vanduzeenia balli	210011001011120100011011000100210011----------1----???010-1-1	1110000-0002212011101000?????
Euptychodera corrugata	210101001111110001010111000111112010001-????1110?0001--10-101	1110000-0002211011101100?????
Odontoscelis fuliginosa	211002111001110100101011000000110011----------0----0??110-101	0010010-00002110010-100001201
Irochrotus maculiventris	20-00211000111011011110100010020-011----------1----01-100-000	0010000-010-2110010-110102202
Hotea curculionoides	0--002001123120021000011000001010010001-0310210001-0020010100	1010011001020110012-10001-2--
Hotea subfasciata	0--00200010310002100001100000100-010001-0310210021-002010-101	1010011000020110010-10001-?--
Deroplax silphoides	0--012000103110020000011000001012010001-03102100100002010-101	0010011001020110112-10001-2--
Deroplax nigrofasciata	0--002001103110021001011000001012010001-0210210011-0020110101	1010011000020110011010001-2--
Tectocoris diophthalmus	0--10000000000000000101000000020-000001-0210111021-002110-0-0	1010010-100001000011100001100
Agonosoma flavolineata	0--002010100020010000111001100110010000-03000001000002011110[01]	001100101-0101100112000103300
Agonosoma trilineatum	0--002010100020010000011001100110010000-03000001000002000-1-[01]	001100101-0101100112000103300
Chelycoris haglundii	0--10220010012000000000100111011001002-0310101013010020010110	0010001100020111012-1000?????
Chelycoris lethierryi	0--10220010002000000000100111011001002-0310101013010020010110	0010001100020111012-3000?????
Chelyschema trinotata	0--10021111001000000101100000011201002-00000000100000201111-0	0010?111?????1???????????????
Diolcus chrysorrhoeus	0--00221110002100000101100000011201002-1010000010000020111101	0011011010020110013-410001?01
Diolcus irroratus	0--00221110002100000101000000011201002-1010000110000020111101	0010011010022110-10-410001101
Diolcus variegatus	0--00201110002100100101100000011201002-10100000101-0020111101	0010011010020110-10-410001101
Orsilochides guttata	0--00201010002000000101100010011001002-001010101301002000-101	0010001100020110012-01001-?--
Orsilochides leucoptera	0--00201110002000000101000010011001002-001010101001002000-101	1010001200020110012-00101-4--
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Polytes tigrinus	0--00001110000100100101100000000100101---0101010100000 2010-101	1010111010120120112-010003302
Polytes velutinus	0--0000111000010000010110000000001001002-1010101010000 0201111-1	1010011310?2012011??3110?????
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Dystus puberulus	20-01020110001000000101100110011011002-01301010130100200111-0	0010001000110110013-100000102
Galeacius martini	0--0002001000100010010101000000110110000-011001010000020111101	0010111110010110010-21001-3--
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Homaemus parvulus	21100221110002000000100000100101001 0001-0310211001-002010-101	0010001100020110110-1110???--
Homaemus proteus	211002201100020000001011001001110010001-0310211001-002010-101	1010001000020110110-111002?01
Crathis ansata	0--1000101010210210010111000000110010011-00000101300002 0111101	001-211200020110010-110000311
Crathis longifrons	0--1000101010210210010101000000110010011-00000101300002 0111101	0011?112?????1???????????????
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Misippus spinolae	0--01021110002100000101100001001 00101---3100110001-00201111-0	0010111110100101002-100002102
Sphyrocoris obliquus	211002201100020000001011000000011201 0001-0010211001-002010-101	1010011000020110110-11011-?--
Symphylus caribbeanus	0--0002101000210100010111000000001001 0002-001001010000020111101	0010111210020110013-400000311
Symphylus cyphonoides	0--0001001000110000010110000000001001 0002-0010010100000201111-0	0010211210020110010-4000?????
Symphylus ramivitta	0--0002001000110000010110000000001001 0002-001001010000020111101	1010011210020110012-400000311
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Tiridates rubroc rubrocinctus	0--002010100020110000011000100010 01002-0110101000000020 00-100	0011-011-----110-1---0-100300
Stethaulax marmorata	0--0022101000200000010110000000001001 0002-001001010000020111101	1010-111-00?01100110?0001-?--

–, inapplicable data; ?, missing data.

Figures

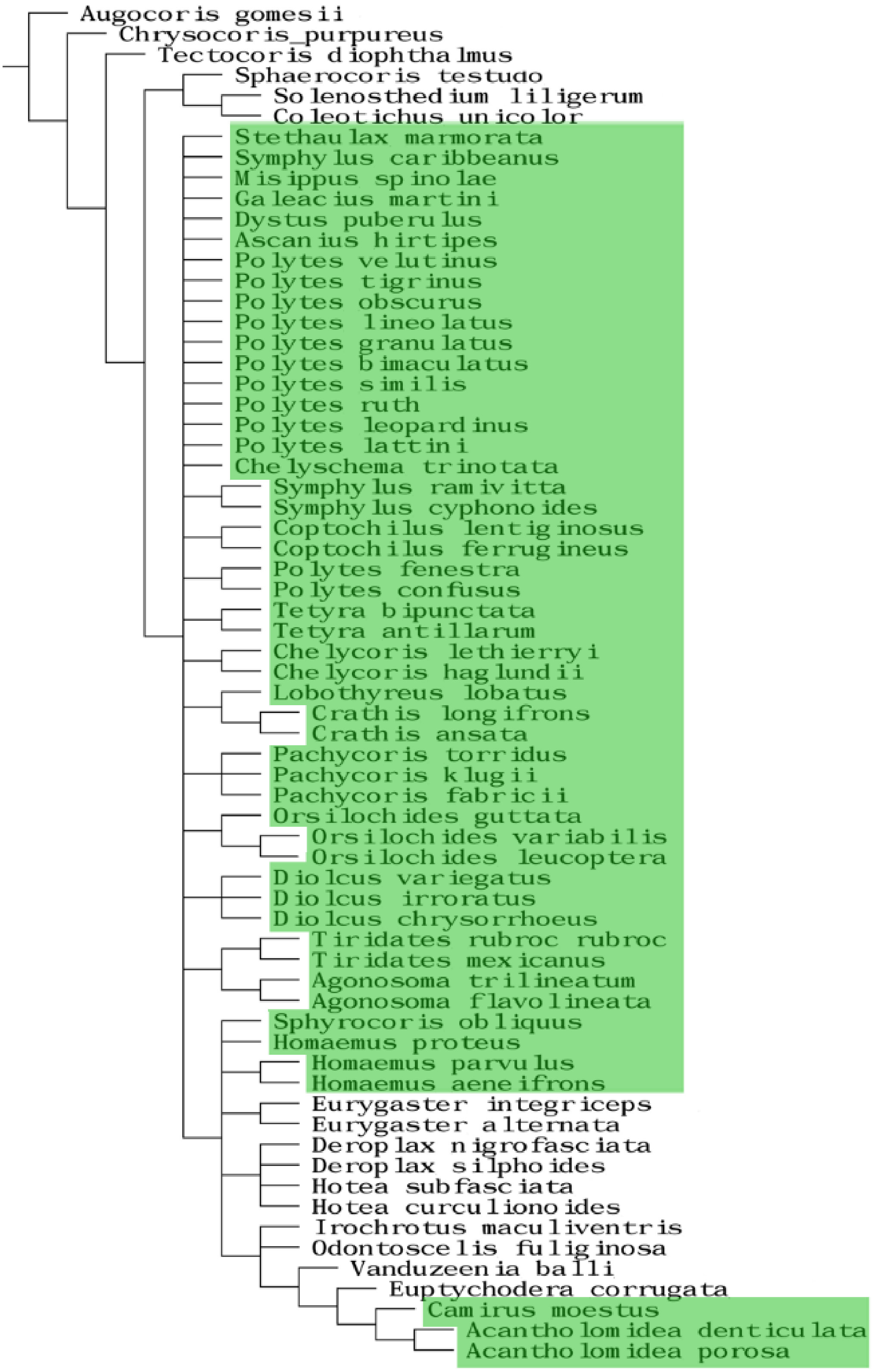

Fig. 1. Cladogram of Pachycorinae resulting consensus tree of most parsimonious trees under equal weights. Color blocks indicate ingroup species.

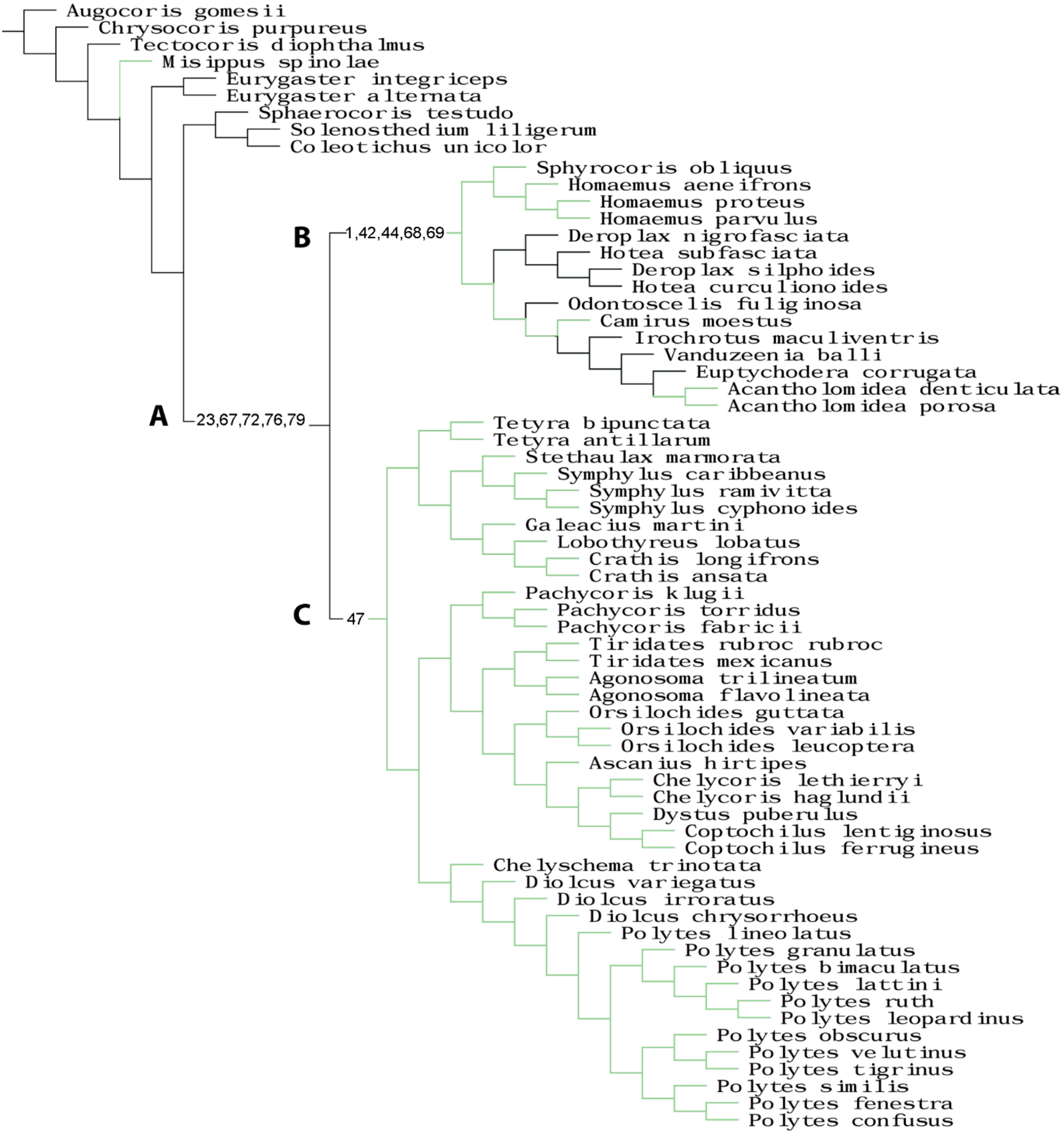

Fig. 2. Cladogram of Pachycorinae resulting tree under implied weights when K = 3. Numbers indicate branch supporting characters. Color branches indicate ingroup species.

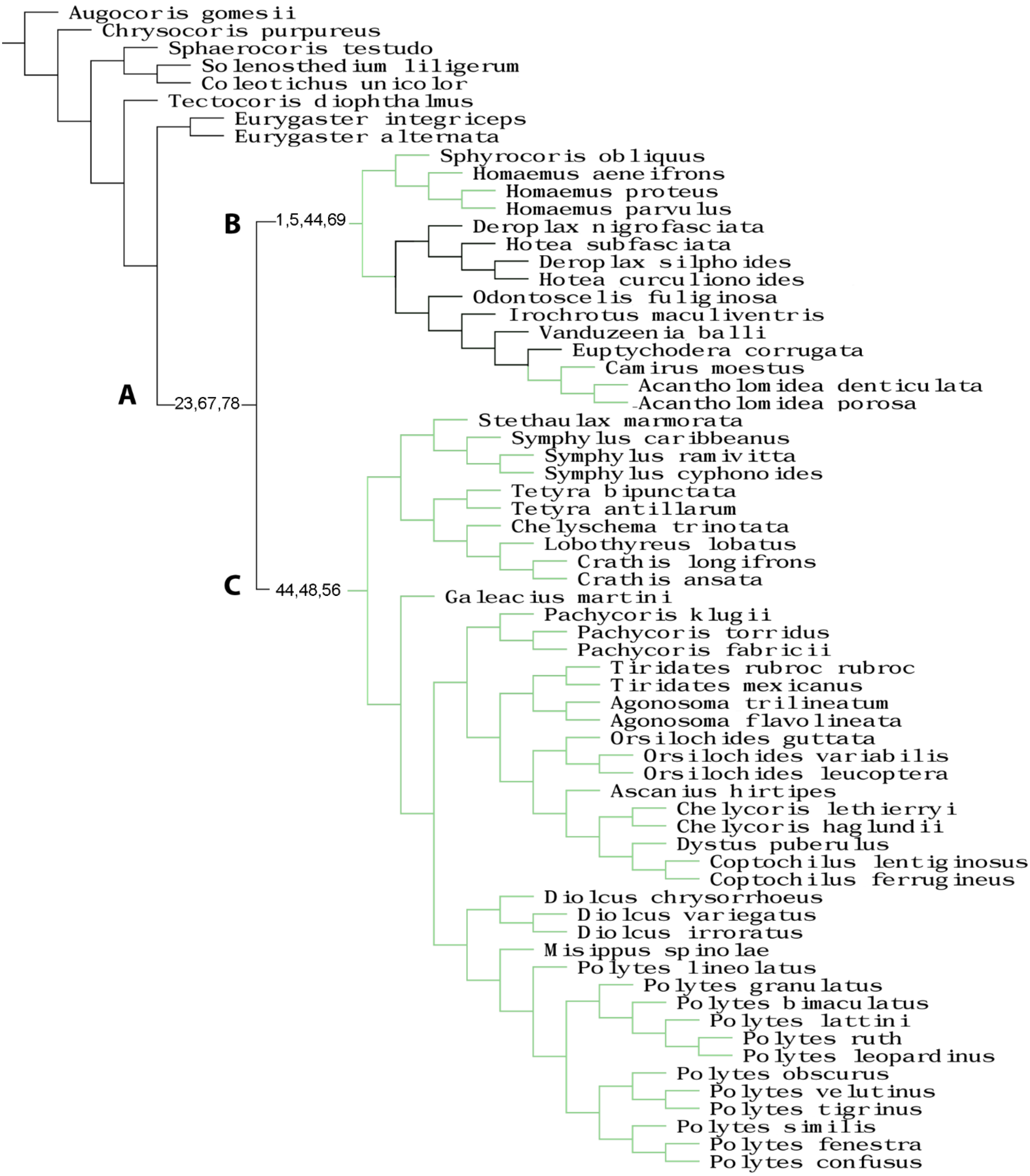

Fig. 3. Cladogram of Pachycorinae resulting tree under implied weights when K = 6. Numbers indicate branch supporting characters. Color branches indicate ingroup species.

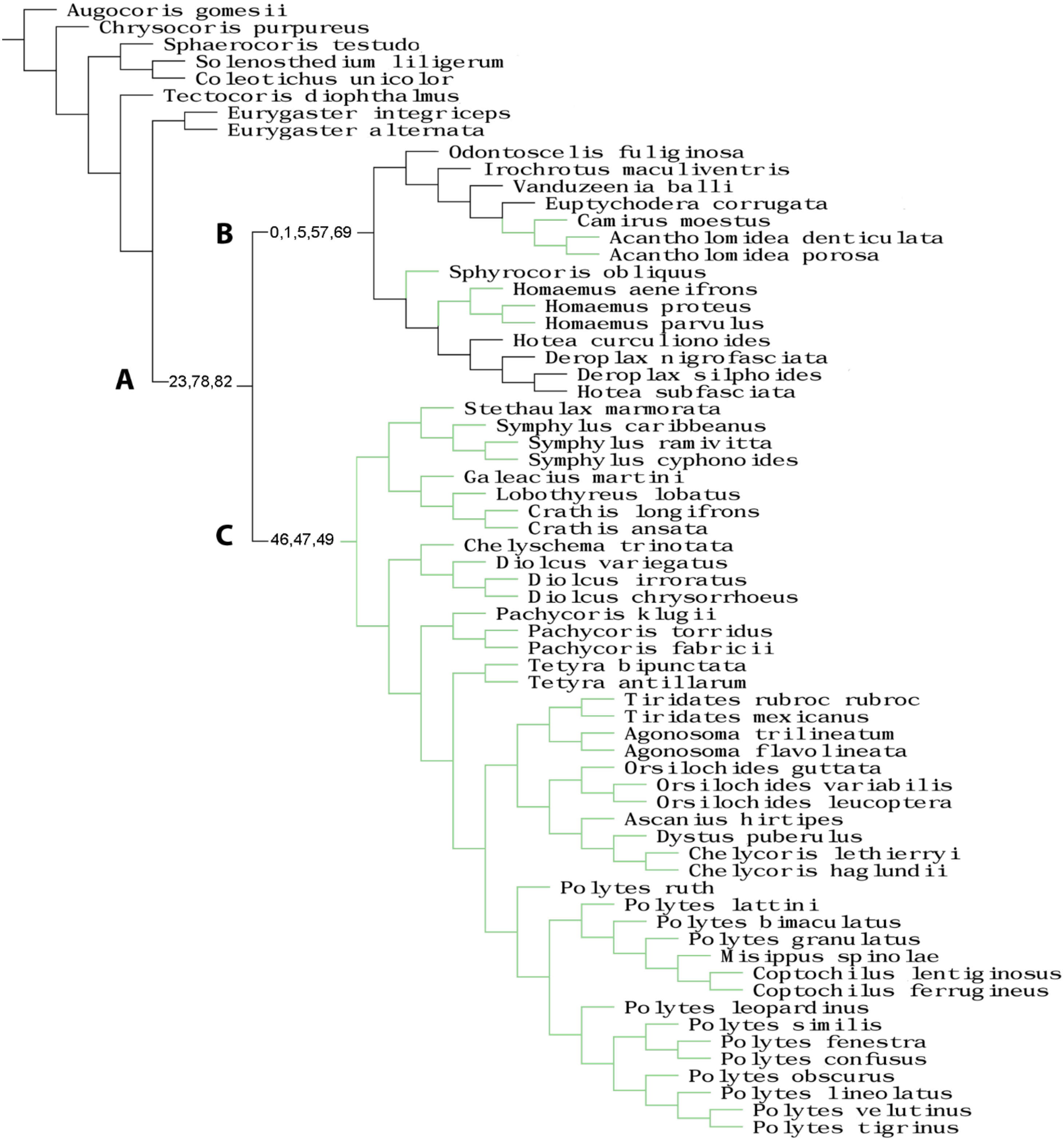

Fig. 4. Cladogram of Pachycorinae resulting tree under implied weights when K = 15. Numbers indicate branch supporting characters. Color branches indicate ingroup species.

CONCLUSÃO GERAL

No capítulo I, estudamos a morfologia externa das glândulas metatorácicas dos gêneros de Pachycorinae através de microscopia eletrônica de varredura. Os gêneros de Pachycorinae têm sido caracterizados por apresentar um sistema eferente odorífero metatorácico pouco desenvolvido. Em contraste, nossos resultados permitiram-nos concluir que a subfamília apresenta um evaporatório bastante desenvolvido e peritrema de pequeno (às vezes obsoleto) à grandemente desenvolvido, particularmente em comparação àqueles observados em outras subfamílias. Encontramos 5 padrões gerais de sistema odorífero externo em Pachycorinae: 1) evaporatório grande e peritrema relativamente bem desenvolvido (*Agonosoma*, *Ascanius*, *Chelycoris*, *Coptochilus*, *Dystus*, *Galeacius*, *Orsilochides*, *Pachycoris*, *Tetyra*, *Tiridates*, *Stethaulax*, e *Symphylus*); 2) evaporatório grande e peritrema fracamente desenvolvido ou obsoleto (*Chelyschema*, *Diolcus*, e *Polytes*); 3) evaporatório reduzido e peritrema pequeno ou obsoleto (*Acantholomidea*, *Camirus*, e *Misippus*); 4) evaporatório reduzido e peritrema longo e bem desenvolvido (*Homaemus* e *Sphyrocoris*) e 5) evaporatório grande e peritrema longo (*Crathis* e *Lobothyreus*). Concordamos com autores prévios que características do sistema odorífero metatorácico são informativas a nível taxonômico de gênero para Scutelleridae e concluímos que os gêneros de Pachycorinae podem ser facilmente reconhecidos através destas características, com exceção de *Crathis* e *Lobothyreus*.

No capítulo II investigamos as relações da subfamília Pachycorinae, através de uma análise cladística para a subfamília Pachycorinae, com base em caracteres morfológicos. A subfamília foi recuperada como parafilética, uma vez que sete gêneros possuem uma relação de parentesco mais próxima com gêneros de outras subfamílias analisadas. Todos os gêneros que tiveram mais de uma espécie incluída na análise foram recuperados como monofiléticos. Nenhuma decisão taxonômica foi realizada, uma vez que se faz necessária exploração de caracteres de genitália de macho e os caracteres de morfologia geral e genitália de fêmea se mostraram bastante homoplásicos. As relações entre as espécies do grupo externo ainda são obscuras e não claramente definidas, uma vez que há frequente flutuação dos terminais entre os clados. Reiteramos a importância da inclusão de caracteres de genitália de macho, bem como mais terminais, para uma mais completa e elucidativa análise das relações filogenéticas entre Scutelleridae. A investigação de caracteres moleculares também seria interessante em futuros estudos filogenéticos da família.

APÊNDICE I

Material suplementar ao Capítulo I

Table 1. List of examined specimens.

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
Acantholomidea	*porosa*	F	United States of America	Florida	Homosassa	Hwy 19	14.IX.2011	J. E. Eger	JEEC
Acantholomidea	*porosa*	F	United States of America	Texas	Austin	Brackenridge Field Laboratory, 170 m	11.IV.1966	C. R. Nelson	MCNZ
Acantholomidea	*porosa*	M	Mexico	Oaxaca	Nilpetec	6mi E; 100 ft	23.VI.1967	S. L. W	MCNZ
Acantholomidea	*denticulata*	M	United States of America	Iowa	Ames		VII.1932	H. M. Harris	DARC
Acantholomidea	*denticulata*	F	United States of America	Iowa	Ames		23.VI.1932	H. M. Harris	DARC
Agonosoma	*flavolineata*	F	Brazil	Mato Grosso do Sul	Aquidauana	Pousada Aguapé ca. 60 km WNW of Aquidauana	21-25.II.2009		MCNZ
Agonosoma	*flavolineata*	F	Brazil	Espírito Santo	Baixo Guandu		18.III.1970	C. T. & C. Elias	DZUP
Agonosoma	*flavolineata*	M	Brazil	Ceará	Carquejo		VI.1960	Dirings	MCNZ
Agonosoma	*trilineatum*	M	Colombia	Tolima		W Mariquita - Fresno; Desvio Entrada Cataratas	23.IV.1993	Semestre	MCNZ

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
						Medina			
Agonosoma	*trilineatum*	F	Venezuela	Aragua	Puerto de Cata		8.VI.1983	S. M. Clark	JEEC
Ascanius	*hirtipes*	M	Argentina	Cordoba	Villa General Belgrano		22.II.2006	D. A. Rider	DARC
Ascanius	*hirtipes*	M	Argentina	Cordoba	Valle Hermoso		07.III.2006	D. A. Rider	DARC
Ascanius	sp.	F	Brazil	Rio Grande do Sul	São Francisco de Paula	FLONA	17-19.XII.2005	L. A. Moura	UFRG
Ascanius	sp.	M	Brazil	Rio de Janeiro	Nova Friburgo	Mury	XII.1975	Gred & Guimarães	MZSP
Camirus	*moestus*	F	Mexico	Hidalgo	Huejutla de Reyes	Xocotitla	28.VIII.1999	E. Barrera	JEEC
Camirus	*moestus*	M	Mexico	San Luis Potosí	Tamasopo		24.VIII.2006	H. Brailovski & E. Barrera	JEEC
Camirus	*moestus*	F	Mexico	Puebla	Izucar de Matamoros		12.X.1989	R. S. Zach	DARC
Camirus	sp.	M	Brazil	Rio Grande do Sul	Porto Alegre		14.III.1960		MGAP
Camirus	sp.	F	Brazil	Rondônia	Ariquemes	62 km SW Ariquemes nr Fzda.	6-15.XII.1990	Rider & J. E. Eger	JEEC

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
						Rancho Grande			
Chelycoris	*haglundi*	F	Brazil	Mato Grosso do Sul	Aquidauana	Pousada Aguapé ca. 60 km WNW of Aquidauana	21-25.II.2009		MCNZ
Chelycoris	*haglundi*	M	Brazil	Mato Grosso do Sul	Aquidauana	Pousada Aguapé ca. 60 km WNW of Aquidauana	21-25.II.2009		MCNZ
Chelycoris	*haglundi*	F	Argentina	Pilcomayo	Clorinda	21 km.W.Clorinda	26.I.1989	C. & L. O'Brien & G. Wibmer	JEEC
Chelycoris	*lethierryi*	M	Brazil	Mato Grosso do Sul	Aquidauana	Pousada Aguapé ca. 60 km WNW of Aquidauana	21-25.II.2009		JEEC
Chelycoris	*lethierryi*	F	Brazil	Mato Grosso do Sul	Aquidauana	Pousada Aguapé ca. 60 km WNW of Aquidauana	21-25.II.2009		JEEC
Chelyschema	*trinotata*	M	Brazil	Santa Catarina	Criciúma		30.IX.2008		MCNZ
Chelyschema	*trinotata*	M	Brazil	Rio Grande do Sul	Tapes	Fazenda Guará	15.V.2003	Equipe Probio	MCNZ
Chelyschema	sp.	F	Brazil	Santa Catarina	Corupá		XI.1957	A. Meller	DZUP

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
Chelyschema	sp.	M	Brazil	Santa Catarina	Corupá		XI.1957	A. Meller	DZUP
Coptochilus	*ferrugineus*	F	Brazil	Rio Grande do Sul	Maquiné	Est. Exp. Fepagro	25.IV.2006	I. Heydrich	MCNZ
Coptochilus	*ferrugineus*	M	Brazil	São Paulo	Campinas		21.III.1985	P. R. Manzani	UFRG
Coptochilus	*ferrugineus*	M	Ecuador	Napo	Puerto Misahualli	vic. Puerto Misahualli, 1650-1900ft.	6-19.IX.1998	J. E. Eger	JEEC
Coptochilus	*lentiginosus*	F	Paraguay	Alto Paraná	Presidente Stroessner	6Km W Pto. Pres. Stroessner	25-28.I.1983	E. G. Riley	JEEC
Coptochilus	*neotropicalis*	M	Guiana Francesa			41Km SE Roura on Kaw Rd.	8.XII.2002	J. E. Eger	JEEC
Crathis	*ansata*	M	Costa Rica	Heredia	Puerto Viejo de Sarapiquí	F. La Selva, 3 km S Pto. Viejo	8.VII.1982	H. A. Hespenheide	MCNZ
Crathis	*ansata*	M	Bolivia	La Paz	Tumupasa		XII.1921-1922	W. M. Mann	MCNZ
Crathis	*ansata*	F	Belize	Cayo		Mile 61, West. Hwy.	10.VIII.1977	L. B. & C. W. O'Brien & G. B. Marshall	MCNZ
Crathis	*longifrons*	M	Bolivia	Beni	Rurrenabaque	Rio Beni	X.1921-1922	W. M. Mann	MCNZ
Crathis	sp.	M	Peru	Huanuco	Tingo Maria	Cueva de las	28.IV.1987	J. Ch. De Vela	MCNZ

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
						Luchuzas S of Tingo Maria			
Diolcus	*irroratus*	F	United States of America	Florida	Tampa		17.II.2002	J. E. Eger	MCNZ
Diolcus	*irroratus*	M	United States of America	Florida	Tampa		24.III.2013	J. E. Eger	JEEC
Diolcus	*irroratus*	M	United States of America	Florida	Big Pine Key		9-14.IV.68	W. R. Enns	DARC
Diolcus	*chrysorrhroeus*	M	United States of America	Texas	College Station		I-IV.1978	J. E. Eger	MCNZ
Diolcus	*variegatus*	F	United States of America	Florida	Homestead		25.IX.2001	J. E. Eger & R. M. Baranowsiki	MCNZ
Dystus	*puberulus*	M	Brazil	Rio Grande do Sul	Triunfo	Parque BRASKEM	4.IV.2009	A. Barcellos & D. Casagrande	MCNZ
Dystus	*puberulus*	M	Brazil	Rio Grande do Sul	Rio Grande	Est. Ecol. TAIM	02.IX.1986	MAL. Marques	MCNZ
Dystus	*puberulus*	F	Brazil	Rio Grande do Sul	Porto Alegre	Belém Novo	I.1959		MGAP
Galeacius	*martini*	M	Brazil	Santa Catarina	Criciúma		2008	F. M. Bianchi	MCNZ
Galeacius	*martini*	F	Brazil	Rio Grande do Sul	São Leopoldo		25.X.1951		MCNZ

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
Galeacius	*martini*	M	Brazil	São Paulo	Itirapina	Est. Exp. Itirapina	26.III.1986	W. R. Silva	UFRG
Homaemus	*aeneifrons*	F	United States of America	West Virginia			25-27.VII.1971	L. H. Rolston	JEEC
Homaemus	*aeneifrons*	M	United States of America	Utah	Grantsville	Camelot's Forest, Boy Scout Campgrnd	25.IX.1991	Rebekah Wagstaff	MCNZ
Homaemus	*aeneifrons*	M	Canada	Quebec	Ste. Hénédine		15.VIII.1986	C. Chantal	JEEC
Homaemus	*parvulus*	M	United States of America	Utah	Cedar Hills		22.VI.1998	S. M. Clark	MCNZ
Homaemus	*proteus*	M	Costa Rica	San Jose	San Jose		12.V.1995	B. O. Huntsman	MCNZ
Homaemus	*bijugis*	F	United States of America	Arizona		Huachuca Montains, Copper Canyon, Montezuma Canyon Rd., 6000ft.	22.VII.2003	S. M. Clark	MCNZ
Lobothyreus	*lobatus*	F	Brazil	Rondônia	Ariquemes	62 km SW Ariquemes nr Fzda. Rancho Grande	5-17.X.1993	J. E. Eger	MCNZ
Lobothyreus	*lobatus*	F	Brazil	Santa Catarina	Nova Teutônia		10.IV.1952	F. Plaumann	MCNZ
Lobothyreus	sp.	M	Brazil	Pará	Santarém				MCNZ

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
Lobothyreus	sp.	M	Brazil	Amazonas	Benjamin Constant	Rio Javari	IX.1962	Dirings	MZSP
Misippus	*spinolae*	F	Brazil	Paraná	Londrina		07.X.2008	F. Siqueira	MCNZ
Misippus	*spinolae*	M	Chile	Elqui	Coquimbo		XII.1993	G. Arriagada	JEEC
Misippus	*spinolae*	M	Argentina	Entre Ríos	Colon		II.1990		DARC
Orsilochides	*variabilis*	F	Belize	Orange Walk	Orange Walk Town	Rio Bravo Cons. Area, La Milpa	11.VII.1996	C. W. & L. B. O'Brien	JEEC
Orsilochides	*variabilis*	M	Mexico	Vera Cruz	Palma Sola		VIII.1972	Reyes & Mahffter	MCNZ
Orsilochides	*variabilis*	M	Honduras	Atlantida	La Celba	Rio Congrajal South	10.VI.1979	Ric Bessin	DARC
Orsilochides	*gutatta*	M	United States of America	Florida	Tampa		21.VIII.1982	J. E. Eger	JEEC
Orsilochides	*leucoptera*	F	Brazil	São Paulo	Campinas		25.XI.1981	L. M. Paleari	UFRG
Orsilochides	*stictica*	M	Mexico	Tamaulipas	Ciudad Victoria	23mi. S. Ciudad Victoria	25.V.1974	C. W. & L. B. O'Brien & Marshall	JEEC
Orsilochides	*scurrilis*	F	Nicaragua	Managua	Managua	Altamira	IX.1970	E. Moore	JEEC
Pachycoris	*torridus*	F							UFRG

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
Pachycoris	*torridus*	F							UFRG
Pachycoris	*torridus*	M	Brazil	Espírito Santo	Baixo Guandu		23-30.XI.1970	C. Elias	DZUP
Pachycoris	*fabricii*	M	Caribbean Netherlands	Saba			2.XII.2006	M. P. K. Yeh	JEEC
Pachycoris	*stalii*	F	Mexico	Baja California Sur	San José del Cabo	ca.200m. E Posada Real Hotel	17.IV.1990	L. H. Williams	UFRG
Pachycoris	*klugii*	M	Mexico	Veracruz	Veracruz	10mi. Ne. Huatusco	29.VI.1971	Clarck, Murray, Hart & Schaffner	UFRG
Polytes	*lineolatus*	M	Peru	Huanuco	Tingo Maria	Cueva de las Luchuzas S of Tingo Maria	21.IX.1988	J. Ch. De Vela	JEEC
Polytes	*lineolatus*	M	Peru	Cuzco	Cuzco	Pilcopata	15.XI.1968	F. Carrasco Z.	UFRG
Polytes	*lineolatus*	M	Ecuador	Napo	Archidona			R. Haensch S.	MZSP
Polytes	*tigrinus*	M	Peru	Huanuco	Tingo Maria	Cueva de las Luchuzas S of Tingo Maria	21.IX.1988	J. Ch. De Vela	MCNZ
Polytes	*lattini*	M	Peru	La Libertad	Cumpang	above Uctubamba	13.X.1979	L. J. Barkley	JEEC

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
						2625 m			
Polytes	*similis*	M	Peru	Huanuco	Tingo Maria	Cueva de Las Luchuzas ,S de Tingo Maria	IV.1988	J. Ch. De vela	JEEC
Polytes	*leopardinus*	M	Peru	Cuzco	Pampaconas		VIII.1911		USNM
Polytes	*velutinus*	M	Colombia	Valle Del Cauca	Dagua				USNM
Sphyrocoris	*obliquus*	F	United States of America	Florida	Plantation Key		15.VI.1982	J. E. Eger	JEEC
Sphyrocoris	*obliquus*	F	United States of America	Travis County	Austin	Brackenridge Field Laboratory	17.VI.1999	C. R. Nelson	MCNZ
Sphyrocoris	*obliquus*	M	Mexico	Tamaulipas	Ciudad Victoria	Hwy 101 16mi.NW.Cd.Victoria 700'	21.VII.1982	C. & L. O'Brien & G. Wibmer	JEEC
Stethaulax	*marmorata*	M	United States of America	California	Santa Barbara	Rattlesnake crk. abv. Skofield prk.	24.I.1985	Baumann-Nelson	JEEC
Stethaulax	*marmorata*	F	United States of America	West Virginia	Old Fields		4-19.VII.2000	W. L. Drosselmeyer	JEEC
Symphylus	*ramivitta*	F	Brazil	Rio Grande do Sul	Triunfo	Parque COPESUL	20.VII.2003	R. Ott & A.	MCNZ

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
								Barcellos	
Symphylus	*ramivitta*	F	Paraguay	Cordillera		Cerro Naranjo	5.III.2005	J. Rives	JEEC
Symphylus	*ramivitta*	M	Brazil	Bahia	Mucuri	BR 101 Km 295	17-22.VI.1968	C. & C. T. Elias	DZUP
Symphylus	*caribbeanus*	F	United States of America	Florida	Lake Placid		28.X.1985	J. E. Eger	JEEC
Symphylus	*cyphonoides*	F	Ecuador	Napo	Puerto Misahualli	1650-1900 ft.	6-19.IX.1998	J. E. Eger	JEEC
Symphylus	sp.	F	Brazil	Rio Grande do Sul	Derrubadas	P.E do Turvo, Trilha Salto Yucumã	19.IV.2004	J. L. C Bernardes	UFRG
Tetyra	*antillarum*	M	Mexico	Chiapas	Ixtapa	Hwy 195 4.5km N Ixtapa 3000'	24.V.1987	D. A. Rider, E. G. & T. J. Riley	JEEC
Tetyra	*antillarum*	F	Caribbean Netherlands	Montserrat		Montserrat: Cassava Ghout, Beattie House	30-V-6-VI.2002	A. Krakon	DARC
Tetyra	*bipunctata*	M	United States of America	Louisiana	Natchitoches		22..IV.1990	D. Rider	DARC
Tetyra	sp.	M	Brazil	Rio Grande do Sul	Sapucaia do Sul	Morro de Sapucaia	3.II.1956		MGAP
Tiridates	*rubrocinctus schaffneri*	M	Honduras	Comayagua	Taulabe	5km NW Taulabe	2.VIII.1977	L. B. & C. W. O'Brien & G. B.	JEEC

Genus	Species	Sex	Country	State/ Province	City	Locality	Date	Collector	Collection
								Marshall	
Tiridates	*rubrocinctus rubrocinctus*	F	Mexico	Campeche	Campeche	89km. NE. Campeche	30.VII.1990	C. W. & L. B. O'Brien	JEEC
Tiridates	*rubrocinctus rubrocinctus*	M	Mexico	Vera Cruz	Catemaco	5 mi. E. Catemaco	2-4.VII.1971	Clark, Murray, Hart & Schaffner	JEEC
Tiridates	*mexicanus*	F	Mexico	Jalisco	Autlan	16 km. n. Autlan	7.VII.1984	Carroll, Schaffner & Friedlander	JEEC

Table 2. Host plants, information source, degree of development of ESES and coloration of Pachycorinae. Evp msem = evaporatorium mesepimeron; Evp mtes = evaporatorium metepisternum; Pe = peritreme.

Genus	Host plants		References	ESES			Coloration
	Family	Species		Pe	Evp mtes	Evp msem	
Acantholomidea Sailer	Fabaceae	*Phaseolus vulgaris* L.	Maes 1994	Short	Reduced	Reduced	Dull, black
Agonosoma Laporte	Convolvulaceae	*Ipomoea batatas* (L.) Lam.	Halmann 1979 Paleari 1992	Long	Enlarged	Enlarged	Dull, red, black and yellow maculae, yellow stripes
	Euphorbiaceae	*Croton glandulosus* L.	Quintanilha et al. 1976				
		Jatropha gossypifolia L.	Rider 2016				
		Cnidosculus urens (L.) Arthur	Smith and Heard 2003				
	Malvaceae	*Gossypium hirsutum* L.					
Ascanius Stål	Rosaceae	*Rubus erythrocladus* Mart.	Barcellos et al. 2014	Long	Enlarged	Enlarged	Dull, light and dark castaneous
Camirus Stål	Asteraceae	*Ambrosia ambrosioides* (Cav.) Payne	Maes 1994 Rider 2016	Short	Reduced	Reduced	Dull, light and dark castaneous
	Malvaceae	*Gossypium* sp.					
Chelycoris Bergroth	Euphorbiaceae	*Croton* sp.	Barcellos et al. 2014	Long	Enlarged	Enlarged	Dull, yellow, light castaneous

Genus	Host plants		References	ESES			Coloration
	Family	**Species**		**Pe**	**Evp mtes**	**Evp msem**	
Chelyschema Bergroth				Short	Enlarged	Enlarged	Dull, reddish and light castaneous
Coptochilus Amiot & Serville					Enlarged	Enlarged	Dull, dark and reddish castaneous
Crathis Stål				Long	Enlarged	Enlarged	Dull, yellow, light and dark castaneous
Diolcus Mayr	Combretaceae Malvaceae	*Conocarpus erectus* L. *Gossypium* sp. *Malvastrum corchorifolium* (Desr.) Britt. *Sida acuta* Burm.	Bruner et al. 1945 Eger and Baranowski 2002 Eger et al. 2015 Wolcott 1941	Short	Enlarged	Enlarged	Dull, reddish, light and dark castaneous
Dystus Stål	Moraceae	*Ficus* spp.	Cervantes-Peredo 2004	Long	Enlarged	Enlarged	Dull, green when alive
Galeacius Distant	Melastomataceae	*Miconia sellowiana* Naudin	Bianchi et al. 2011	Long	Enlarged	Enlarged	Dull, yellow, light and dark castaneous
Homaemus Dallas				Long	Enlarged	Reduced	Dull, light and dark castaneous
Lobothyreus Mayr				Long	Enlarged	Enlarged	Dull, yellow, light, dark and reddish castaneous

Genus	Host plants		References	ESES			Coloration
	Family	**Species**		**Pe**	**Evp mtes**	**Evp msem**	
Misippus Stål	Poaceae	*Oryza sativa* L. *Sorghum bicolor* (L.) Moench	Quintanilla et al. 1976	Obsolete	Reduced	Reduced	Dull, light and reddish castaneous
Orsilochides Kirkaldy	Euphorbiaceae Malvaceae Poaceae	*Croton* sp. *Jatropha curcas* L. *Gossypium hirsutum* L. Moench *Sorghum bicolor* (L.)	Barcellos et al. 2014 Quintanilha et al. 1976 Grimm and Maes 1997	Long	Enlarged	Enlarged	Dull or bright; light and dark castaneous, yellow, orange, black and metallic-green maculae
Pachycoris Burmeister	Anarcadiaceae Aquifoliaceae Boraginaceae	*Anacardium occidentale* L. *Mangifera indica* L. *Schinus terebinthifolius* Raddi *Ilex paraguayensis* St. Hil. *Cordia nitida* Vahl. *Cordia* sp.	Barber 1939 Bosq 1937, 1940 Callan 1948 Cervantes-Peredo 2002 Costa Lima 1928, 1940	Long	Enlarged	Enlarged	Dull, full body black, red or castaneous; with yellow, orange, red, black or metallic-blue maculae

Genus	Host plants		References	ESES			Coloration
	Family	Species		Pe	Evp mtes	Evp msem	
	Euphorbiaceae	*Aleurites fordii* Hernst. *Cnidosculus pubescens* Pohl *Croton californicus* Müll. Arg *C. discolor* (Willd.) Raf. *C. humilis* L. *Croton* sp. *Jatropha curcas* L. *Jatropha* sp. *Manihot esculenta* L. *Sapium haematospermum* Müll. Arg.	Guimarães 1977 Hussey 1934 Maes 1994 Martínez-Herrera et al. 2010 Michelotto et al. 2006 Rider 2016 Rodrigues et al. 2011 Sanchez-Soto et al. 2004 Santos et al. 2005 Sánchez-Soto and Nakano 2002				
	Malpighiaceae	*Malpighia glabra* L.	Souza et al. 2012				
	Myrtaceae	*Eucalyptus* sp. *Psidium guajava* L. *P. guineense* Sw.	Tepole-García et al. 2012 Williams et al. 2005				

Genus	Host plants		References	ESES			Coloration
	Family	Species		Pe	Evp mtes	Evp msem	
	Poaceae	*Oryza sativa* L.	Wolcott 1923, 1941				
	Rubiaceae	*Coffea* sp.					
	Verbenaceae	*Lantana involucrata* L.					
		Lantana sp.					
Polytes Stål				Obsolete	Enlarged	Enlarged	Dull, black, light and dark castaneous, red, orange and yellowish maculae, yellow stripes
Sphyrocoris Mayr	Asteraceae	*Bidens bipinnata* L.	Callan et al. 1948	Long	Enlarged	Reduced	Dull, light and dark castaneous
		Bidens sp.	Crawford 1913				
	Lamiaceae	*Salvia mellifera* Greene	Eger 2012				
	Malvaceae	*Gossypium barbadense* L.	Grimm and Maes 1997				
	Fabaceae	*Glycine max* L. Merrill					
	Euphorbiaceae	*Jatropha curcas* L.					
Stethaulax Bergroth				Long	Enlarged	Enlarged	Dull, light and dark castaneous
Symphylus Dallas	Anacardiaceae	*Magifera indica* L.	Blatchley 1926	Long	Enlarged	Enlarged	Dull, light and dark castaneous, reddish, yellowish, yellow stripes
	Boraginaceae	*Cordia macrostachya* (Jacquin) Roemer &	Bruner et al. 1945 Callan et al. 1948				

Genus	Host plants		References	ESES			Coloration
	Family	Species		Pe	Evp mtes	Evp msem	
		Schultes	Eger et al. 2015				
	Clusiaceae	*Clusia major* L.	Lattin 1964				
	Fabacaeae	*Phaseolus lathyroides* L.	McPherson 1977				
	Lamiaceae	*Salvia mellifera* Greene	Rider 2016				
	Malvaceae	*Hibiscus rosa-sinensis* L.	Torre-Bueno 1914				
	Myricaceae	*Myrica cerifera* L.	Uhler 1894				
Tetyra Fabricius	Fabaceae	*Acacia caven* (Mol.) Mol.	Berg 1879	Long	Enlarged	Enlarged	Dull, light and dark castaneous
		A. farnesiana (L.) Willd.	Maes 1994				
		Gleditsia triacanthos L.	Wolcott 1941				
	Rubiaceae	*Coffea* sp.					
	Solanaceae	*Solanum bonariense* L.					
Tiridates Stål				Long	Enlarged	Enlarged	Dull, orange, yellow, black

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ANEXO I

NORMAS PARA PUBLICAÇÃO

ZOOMORPHOLOGY

Types of papers

The journal publishes Original papers, Reviews and Method Papers.

Original papers should present substantial new results that have never been published or submitted elsewhere; they should not exceed 10 printed pages (one printed page corresponds to approximately: 850 words text, or 3 illustrations with their legends, or 55 references) and should be arranged as detailed below.

Reviews should not exceed 25 printed pages. Please contact the Editor-in-Chief prior to submission.

Method Papers should present new approaches or reviews on methods used in animal morphology. They should not exceed 10 printed pages.

Manuscript Submission

Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

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Please follow the hyperlink “Submit online” on the right and upload all of your manuscript files following the instructions given on the screen.

Cost of Color Illustrations

- Online publication of color illustrations is always free of charge.

- For color in the print version, authors will be expected to make a contribution towards the extra costs of EUR 950 / US$ 1150 (+ local tax) per article, irrespective of the number of figures in it.

Suggesting Reviewers

While submitting your paper you will be asked to suggest three potential reviewers. Indicating three reviewers is mandatory.

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Manuscripts that are accepted for publication will be checked by our copyeditors for spelling and formal style. This may not be sufficient if English is not your native language and substantial editing would be required. In that case, you may want to ask a native speaker to help you or arrange for your manuscript to be checked by a professional language editor prior to submission. A clear and concise language will help editors and reviewers concentrate on the scientific content of your paper and thus smooth the peer review process.

The following editing service provides language editing for scientific articles in medicine, biomedical and life sciences, chemistry, physics, engineering, business/economics, and humanities

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Please contact the editing service directly to make arrangements for editing and payment.

Use of an editing service is neither a requirement nor a guarantee of acceptance for publication.

Title Page

The title page should include:

- The name(s) of the author(s)
- A concise and informative title
- The affiliation(s) and address(es) of the author(s)
- The e-mail address, telephone and fax numbers of the corresponding author

Abstract

Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

Keywords

Please provide 4 to 6 keywords which can be used for indexing purposes.

Text Formatting

Manuscripts should be submitted in Word.

- Use a normal, plain font (e.g., 10-point Times Roman) for text.
- Use italics for emphasis.
- Use the automatic page numbering function to number the pages.
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).

Manuscripts with mathematical content can also be submitted in LaTeX.

- LaTeX macro package (zip, 182 kB)

Headings

Please use no more than three levels of displayed headings.

Abbreviations

Abbreviations should be defined at first mention and used consistently thereafter.

Footnotes

Footnotes can be used to give additional information, which may include the citation of a reference included in the reference list. They should not consist solely of a reference citation, and they should never include the bibliographic details of a reference. They should also not contain any figures or tables.

Footnotes to the text are numbered consecutively; those to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data). Footnotes to the title or the authors of the article are not given reference symbols.

Always use footnotes instead of endnotes.

Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

Specific Remarks

Please arrange your manuscript as follows:

- Introduction

  The Introduction should be brief and state the purpose of the work in relation to other work in the same field. It should not present an extensive review of the literature and contain the scientific question or testable hypothesis that led to the study.

- The Materials and methods

  This section should provide enough information to permit repetition of the experimental work.

- Results

  This section should present the findings of the research, supported by statistical or illustrative validation of the assertions. It should be free of discussion.

- Discusion

  The Discussion should cover but not simply repeat the new findings presented in Results, setting these in context and interpreting them with a minimum of speculation. It should refer to the question/hypothesis mentioned in the Introduction.

Scientific style

- Genus and species names should be in italics.
- Authors of scientific names of the genus and species group should not be italicized; they are not to be abbreviated.
- Nomenclature

  Names for higher taxa should refer to monophyletic units, not to paraphyla (use, e.g., Teleostei or Plathelminthes but not designations such as Pisces or Turbellaria). International nomenclature conventions must be observed, especially the International

Code of Zoological Nomenclature (IRZN). At first mention, a specific name should be cited with nomenclatural author and year, e.g. Catenula lemmnae (in italics) Dugès, 1832. Authors unfamiliar with the taxonomy of the group to which a species belongs should consult an expert to ensure that it is properly identified and that the correct name is used.

References

Citation

Cite references in the text by name and year in parentheses. Some examples:

- Negotiation research spans many disciplines (Thompson 1990).
- This result was later contradicted by Becker and Seligman (1996).
- This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

Reference list

The list of references should only include works that are cited in the text and that have been published or accepted for publication. Personal communications and unpublished works should only be mentioned in the text. Do not use footnotes or endnotes as a substitute for a reference list.

Reference list entries should be alphabetized by the last names of the first author of each work. Order multi-author publications of the same first author alphabetically with respect to second, third, etc. author. Publications of exactly the same author(s) must be ordered chronologically.

- Journal article

  Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. Eur J Appl Physiol 105:731-738. doi: 10.1007/s00421-008-0955-8

  Ideally, the names of all authors should be provided, but the usage of “et al” in long author lists will also be accepted:

  Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. N Engl J Med 965:325–329

- Article by DOI

  Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. doi:10.1007/s001090000086

- Book

  South J, Blass B (2001) The future of modern genomics. Blackwell, London

- Book chapter

  Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257

- Online document

  Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007

- Dissertation

  Trent JW (1975) Experimental acute renal failure. Dissertation, University of California

Always use the standard abbreviation of a journal’s name according to the ISSN List of Title Word Abbreviations, see

- ISSN LTWA

If you are unsure, please use the full journal title.

For authors using EndNote, Springer provides an output style that supports the formatting of in-text citations and reference list.

- EndNote style (zip, 2 kB)

Tables

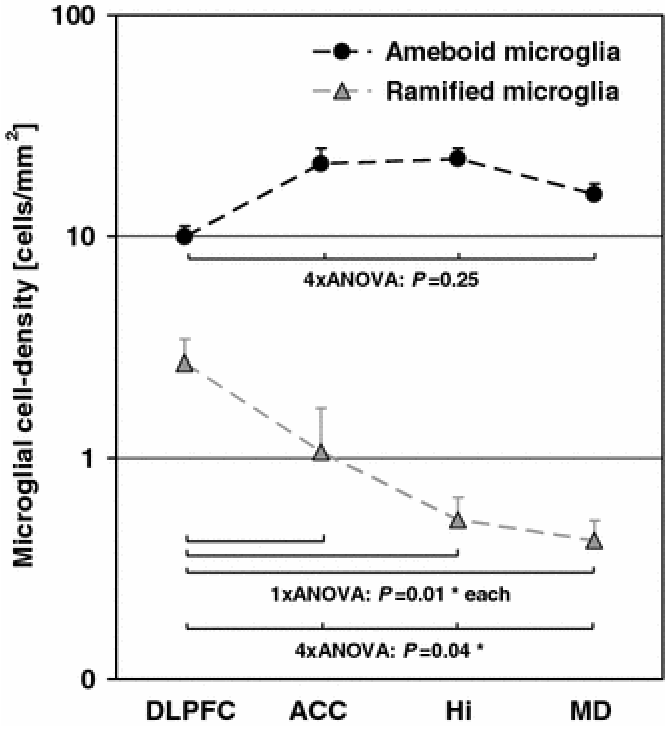
- All tables are to be numbered using Arabic numerals.
- Tables should always be cited in text in consecutive numerical order.
- For each table, please supply a table caption (title) explaining the components of the table.
- Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
- Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

Artwork and illustration guidelines

Electronic Figure Submission

- Supply all figures electronically.
- Indicate what graphics program was used to create the artwork.
- For vector graphics, the preferred format is EPS; for halftones, please use TIFF format. MSOffice files are also acceptable.
- Vector graphics containing fonts must have the fonts embedded in the files.
- Name your figure files with "Fig" and the figure number, e.g., Fig1.eps.

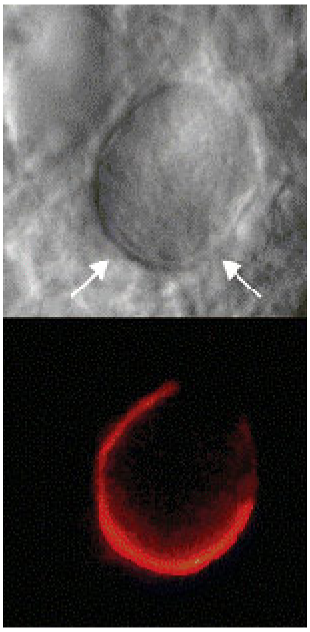
Line Art



- Definition: Black and white graphic with no shading.

- Do not use faint lines and/or lettering and check that all lines and lettering within the figures are legible at final size.
- All lines should be at least 0.1 mm (0.3 pt) wide.
- Scanned line drawings and line drawings in bitmap format should have a minimum resolution of 1200 dpi.
- Vector graphics containing fonts must have the fonts embedded in the files.

Halftone Art



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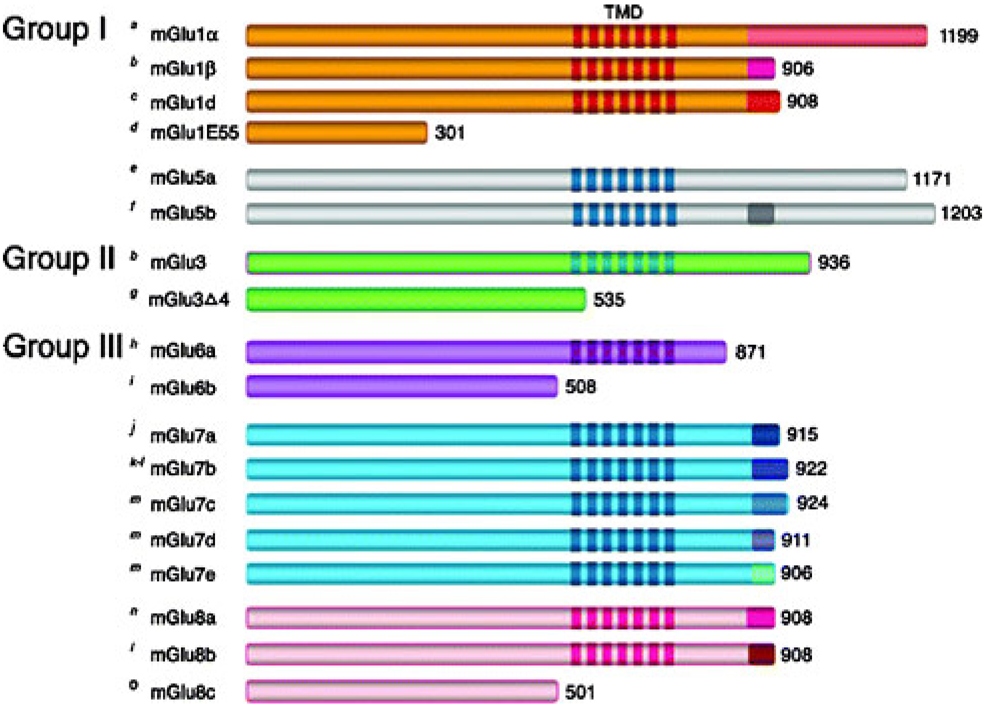
- If any magnification is used in the photographs, indicate this by using scale bars within the figures themselves.
- Halftones should have a minimum resolution of 300 dpi.

Combination Art



- Definition: a combination of halftone and line art, e.g., halftones containing line drawing, extensive lettering, color diagrams, etc.
- Combination artwork should have a minimum resolution of 600 dpi.

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- Color art is free of charge for online publication.
- If black and white will be shown in the print version, make sure that the main information will still be visible. Many colors are not distinguishable from one another when converted to black and white. A simple way to check this is to make a xerographic copy to see if the necessary distinctions between the different colors are still apparent.
- If the figures will be printed in black and white, do not refer to color in the captions.
- Color illustrations should be submitted as RGB (8 bits per channel).

Figure Lettering

- To add lettering, it is best to use Helvetica or Arial (sans serif fonts).
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- Figures should always be cited in text in consecutive numerical order.
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References. In the text, references are cited chronologically by the author and date and are not numbered. Names of two coauthors are linked by ´and´; for three or more, the first author´s name is followed by ´*et al.*´. Citation of authorities (name and date) should be given when a taxon name is first mentioned. Two or more coauthors of a name are linked by ´&´. All references cited must be listed alphabetically at the end of the paper; all entries in this list must correspond to references in the text. No editorial responsibility can be taken for the accuracy of the references and authors are requested to check these with special care. Titles must be included for all references. Papers that have not been accepted for publication may not be included in the list of references and must be cited either as ´unpublished data´ or as ´personal communication´; the use of such citations is discouraged. Authors are referred to the latest issues of the Journal for the style to be used in citing references to books and other literature. **Titles of periodicals must not be abbreviated.**

EndNote and Reference Manager provide output styles for **Invertebrate Systematics**. References should be in the following formats:

- Haswell, W. A. (1882). ´Catalogue of the Australian Stalk- and Sessile-eyed Crustacea.´ (Australian Museum: Sydney, Australia.)
- Sluys, R., and Ball, I. R. (1988). A synopsis of the marine triclads of Australia and New Zealand (Platyhelminthes : Tricladida : Maricola). *Invertebrate Taxonomy* **2**, 915-959.
- Voss, G. L. (1988). Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In ´The Mollusca. Vol. 12. Palaeontology and Neontology of Cephalopods´. (Eds M. R. Clarke and E. R. Trueman.) pp. 253-276. (Academic Press: London, UK.)
- Erzinçlioglu, Y. Z. (1984). ´Studies on the Morphology and Taxonomy of the Immature stages of Calliphoridae, with Analysis of Phylogenetic Relationships within the Family, and Between It and Other Groups in the Cyclorrhapha (Diptera).´ PhD thesis., (University of Durham:, UK.)
- Huelsenbeck, J. P., and Ronquist, F. (2001). ´MrBayes 2.01: Bayesian Inference of Phylogeny.´ Available at http://morphbank.ebc.uu.se/mrbayes/.

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Each table (including data matrices and character lists, where appropriate) must be numbered with arabic numerals and must be accompanied by a title. A headnote containing material relevant to the whole table should start on a new line, as it will be set in a different font. Tables should be arranged with regard to the dimensions of the printed page (17.5 by 22.5 cm in two 8.5-cm columns) and the number of table columns kept to a minimum. Excessive subdivision of column headings is undesirable and long headings should be avoided by the use of explanatory notes, which should be incorporated into the headnote. Footnotes should be kept to a minimum and reserved for specific items in columns. Horizontal rules should be inserted only above and below the column headings and at the foot of the table. Vertical rules must not be used. Each table must be referred to in the text. Only in exceptional circumstances will the presentation of essentially the same data in both tabular and graphical form be permitted; where adequate, the graphical form should be used. Short tables can frequently be incorporated into the text as a sentence or as a brief untitled tabulation.

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