Zoological Studies **60**:11 (2021)
doi:10.6620/ZS.2021.60-11

Zoological Studies

Open Access

Finding *Padaeus bovillus* (Hemiptera: Pentatomidae): A Phylogenetic Placement and the Description of Its Sister Species

Filipe Michels Bianchi[1,*], Verônica Krein[1], David Rider[2], and Jocelia Grazia[1]

[1]*Laboratório de Entomologia Sistemática, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil. *Correspondence: E-mail: bianchi.fm@hotmail.com (Bianchi)*
E-mail: vero.krein@hotmail.com (Krein); jocelia@ufrgs.br (Grazia)
[2]*Entomology Department, School of Natural Resource Sciences, North Dakota State University, Fargo, ND, USA.*
E-mail: david.rider@ndsu.edu (Rider)

Received 28 November 2020 / Accepted 14 January 2021 / Published 22 March 2021
Communicated by Y. Miles Zhang

The pentatomids (Hemiptera: Heteroptera) are the third most speciose family within the Heteroptera or the true bugs. The family occurs worldwide and comprises around five thousand valid species within 950 genera. *Padaeus* Stål belongs to a complex of other genera of Carpocorini Mulsant and Rey related to *Euschistus* Dallas. These genera present similarities in color, size, and shape, and share common features. However, among its four congeneric species, *Padaeus bovillus* Distant has been highlighted as an outlier by the posterior margins of the bucculae evanescent, while its congeneric species present posterior margins of the bucculae lobed. Thus, herein we redescribe *P. bovillus* and present a hypothesis regarding its phylogenetic placement within the Carpocorini. Furthermore, a new species similar to *P. bovillus* is described. Four molecular markers (*COI*, CytB, 16S, and 28S) plus 86 morphological characters were used to infer the phylogeny under Maximum likelihood and Bayesian inference. For the descriptions, we measured 16 morphometric parameters and dissected the genitalic structures. We also include illustrations of the habitus, internal and external genitalic structures, and provide distribution maps. *Mitripus seclusus* sp. n. Bianchi, Krein, Rider, and Grazia is recovered as the sister species to *Mitripus bovillus* comb. n., and both within *Mitripus* Rolston. Among other shared characters, species of *Mitripus* have the femora unarmed, they have a macula near the apex of the radial vein, and the mandibular plates tapering apically. *Mitripus bovillus* comb. n. and *Mitripus seclusus* sp. n. have the posterior margin of the pygophore projecting as a spine, a unique pattern within the genus. According to our results, *Mitripus* including *M. bovillus* comb. n. and *Mitripus seclusus* sp. n. now includes five species.

Key words: Carpocorini, Pentatominae, Phylogenetics, Stink bug, Neotropics.

BACKGROUND

Within Heteroptera (Insecta: Hemiptera), Pentatomidae is one of the three largest families (Schuh and Weirauch 2020). Pentatomids are known as stink bugs, and the family contains about 950 genera containing almost 5,000 valid species (Rider et al. 2018). Although well-supported monophyly of Pentatomidae has been inferred using distinct sources of data and analytical approaches, the phylogenetic relationships within the family are still unclear (*e.g.*, Henry 1997; Li et al. 2005; Grazia et al. 2008; Wu et al. 2016). For the subordinate taxa within Pentatomidae, phylogenetic hypotheses are scarce (Grazia et al. 2008). The taxonomy and classification of Pentatomidae have mostly been based on morphological similarities. Thus, most tribes and groups of genera have never been studied under a phylogenetic framework, and

Citation: Bianchi FM, Krein V, Rider D, Grazia J. 2021. Finding *Padaeus bovillus* (Hemiptera: Pentatomidae): A phylogenetic placement and the description of its sister species. Zool Stud **60**:11. doi:10.6620/ZS.2021.60-11.

the relationships within the family lack phylogenetic hypotheses (Rider et al. 2018).

Euschistus Dallas is currently placed in Carpocorini Mulsant and Rey, and it is one of the most speciose genera within the Pentatomidae, containing 67 species (Bianchi et al. 2017a), all of which occur exclusively in the New World (Rolston 1974a). The delimitation of the genus is imprecise, resulting in a considerable progressive accretion of species since its proposition, and also a subsequent creation of new genera for species formerly placed within *Euschistus* (*e.g.*, *Ladeaschistus* Rolston, *Adustonotus* Bianchi) (Rolston 1974a; Bianchi et al. 2017a). Moreover, during the taxonomic history of the Pentatomidae, many genera have been hypothesized to be related to *Euschistus* (*Euschistus* group, hereafter), mainly due to morphological similarities and distribution. Barão et al. (2020) recovered the monophyly of the *Euschistus* group containing 22 genera.

Padaeus Stål is one of the genera that Rolston (1974a) speculated might be related to *Euschistus*; and its placement of *Padaeus* within *Euschistus* group was hypothesized by Barão et al. (2020). Currently, *Padaeus* includes *P. bovillus* Distant, *P. teapensis* (Distant), *P. trivittatus* Stål, *P. verrucifer* Stål, and the type species *P. viduus* (Vollenhoven). A diagnostic character of *Padaeus* is the posterior margins of bucculae are lobed and prolonged to the base of the head (Stål 1862; Rolston 1974a; Rolston and McDonald 1984). However, this feature is not common to all species of *Padaeus*. *Padaeus bovillus* has the posterior margins of the bucculae evanescent, similar to many other species of *Euschistus* group. This condition has put the current placement of *P. bovillus* in question (*e.g.*, Rolston 1974a; Rolston and McDonald 1984). Even in the original description, Distant (1900) stated that *P. bovillus* differs from its congeneric species and highlighted its resemblance to *Sibaria armata* (Dallas).

From an in-depth investigation of the morphology of specimens identified as *P. bovillus*, we discovered that some specimens differed slightly in general somatic characters, and greatly in genitalic structures. Thus, we provide a phylogenetic hypothesis for the systematic placement of *P. bovillus* and the similar species found by us, redescribe *P. bovillus* and update the knowledge of this species, and describe the new species similar to *P. bovillus*.

MATERIALS AND METHODS

Phylogenetic analyses

Bianchi et al. (2017b) provided a backbone for the phylogenetic relationships among genera related to *Sibaria* and *Ladeaschistus*. Thus, we used the morphological and molecular matrices of Bianchi et al. (2017b) to serve as the base for our phylogenetic analyses. This matrix contained 32 taxa scored for 85 morphological characters and 2327 bp from the mitochondrial markers cytochrome c oxidase subunit I (*COI*), cytochrome *b* (Cytb) and ribosomal 16S, and 28S. Since our focus was to accommodate *P. bovillus* and a new species, the matrix was reduced to 21 terminal taxa, and *P. viduus* (the type species of *Padaeus*), the recently described *Sibaria amazonica* Krein, Rider & Grazia (see DISCUSSION), *P. bovillus* and the new species (Table 1) were added. The selection of terminal taxa prioritized availability of molecular data, although we kept the generic sampling.

We also proposed an additional morphological character (*i.e.*, character 11: Head, proportion of eyes related to head width: (0) less than 0.43; (1) greater than 0.5), and a new state to character 68 (*i.e.*, Pygophore, ventral rim at middle, form: (5) pointed). Both states for each character were re-evaluated and the scores of the whole matrix were double-checked (Table S1). The specimens used to score the morphological matrix were identified according to the literature (Table 1).

The specimens of *S. amazonica*, *P. viduus*, *P. bovillus* and the new species were preserved on pins; they were collected many decades ago (see material examined). The genomic DNA extractions followed Bianchi et al. (2017b) protocol using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA). The results, however, were of low quality and quantity. Therefore, only the morphological partition was scored for *S. amazonica*, *P. viduus*, *P. bovillus* and the new species. The other four molecular partitions were scored as missing data for these species. Morphological data were coded in Mesquite 3.61 (Maddison and Maddison 2019), and the matrix was exported as a NEXUS file for phylogenetic analyses. Unobserved states were scored with '?' and inapplicable states with '–'. All characters were treated as nonadditive (Table 2). Morphological characters analyzed using probabilistic methods were treated under the Mk evolutionary model (Lewis 2001). The alignments of individual molecular markers, evolutionary models for each partition, maximum-likelihood routine (ML) including bootstrap (BS), and other parameters not stated here followed Bianchi et al. (2017b).

Bayesian inference (BI) using the concatenated matrix was performed in the multithreading version of the program MrBayes 3.2.0 (Ronquist and Huelsenbeck 2003), setting nst = 1 rates = equal for morphological partition and nst = 6 rates = invgamma for each molecular marker, for 2.5 million generations (nruns = 2

nchains = 4) with trees sampled every 1000 generations. Tracer v.1.6.0 (Rambaut et al. 2014) was used to inspect the convergence with the stationary distribution of the chains. The first 20% of the generations were discarded as "burn-in", and then the chains were combined. The combined ESS values for each parameter were higher than 200. The posterior probability (PP) was estimated for the remaining generations. For both ML and BI values, the nodes presenting PP < 0.50 and BS < 50 were collapsed. Phylogenetic trees were visualized and edited using FigTree v1.4.0 (Rambaut et al. 2014) (http://tree.bio.ed.ac.uk/software/figtree/). *Glyphepomis spinosa* Campos & Grazia was used to root the trees in both ML and BI analyses based on Bianchi et al. (2017b) and Barão et al. (2020).

Taxonomy

All the specimens were observed and evaluated using a light stereomicroscope. The measurements of the following 15 morphometric parameters were taken under a light stereomicroscope: total body length (BL) (measured from the apex of head to the apex of the abdomen, excluding the hemelytral membranes), maximum abdominal width (AW), medial length of head (HL) (disc of the head parallel to observer), maximum width of head (HW) (including eyes), length of head anterior to the eyes (LE), interocular distance (ID), length of antennomeres I (I), II (II), III (III), IV (IV), V (V), medial pronotal length (PL), maximum pronotal width (PW), medial scutellar length (SL), and maximum scutellar width (SW). Measurements (mean ± standard deviation) were given in millimeters.

The entire abdomen was removed from each female to access the internal genitalia. For males, only the pygophore was removed. Each female abdomen and male pygophore was then cleaned in aqueous supersaturated KOH solution and boiled for about 10 minutes. Female internal genitalic structures were stained with Congo Red. The terminology of genitalic structures follows Baker (1931), Dupuis (1970), and Schaefer (1977), and Tsai et al. (2011) exclusively for parameres. Kment and Vilímová (2010) were followed for terminology concerning the external scent efferent system of the metathoracic scent glands. Macrophotographs of dorsal, ventral and lateral habitus,

Table 1. Taxon sampling for the phylogenetic analysis of *Padaeus bovillus* (Distant) and related carpocorines, including Genbank accession number for respective DNA marker. Molecular markers not sequenced marked with "-". Identification literature brings the main reference used to identify specimens used in the morphological analysis

Species	*COI*	Cyt b	16S	28S	Identification literature
Adustonotus grandis (Rolston)	KU892549	KU853795	KU853775	KU853759	Bianchi et al. 2017b
Adustonotus hansi (Grazia)	KU892550	KU853796	-	KU853760	Bianchi et al. 2017b
Adustonotus saramagoi (Bianchi, Cioato and Grazia)	KU892552	KU853798	KU853778	-	Bianchi et al. 2017b
Adustontous paranticus (Grazia)	KU892551	KU853797	KU853777	KU853761	Bianchi et al. 2017b
Agroecus scabricornis (Herrich-Schäffer)	KU892539	KU853783	KU853764	-	Rider and Rolston 1987
Caonabo pseudoscylax (Bergroth)	KU892540	KU853784	KU853765	KU853749	Rolston 1974b
Diceraeus furcatus (Fabricius)	U892541	KU853785	KU853766	KU853750	Barão et al. 2020
Dichelops (*D.*) *leucostigmus* (Dallas)	U892542	KU853786	KU853767	KU853751	Barão et al. 2020
Euschistus (*E.*) *crenator* (Fabricius)	-	KU853787	KU853768	KU853752	Rolston 1974a
Euschistus (*E.*) *heros* (Fabricius)	KU892543	KU853788	KU853769	KU853753	Rolston 1974a
Euschistus (*E.*) *taurulus* Berg	KU892545	KU853789	KU853770	KU853754	Hickmann et al. 2019
Euschistus (*L.*) *circumfusus* Berg	-	KU853790	KU853771	KU853755	Weiler et al. 2016
Euschistus (*L.*) *cornutus* (Dallas)	U892546	KU853791	KU853772	KU853756	Weiler et al. 2016
Euschistus (*L.*) *triangulator* (Herrich-Schäffer)	-	KU853792	KU853773	KU853757	Weiler et al. 2016
Glyphepomis spinosa Campos and Grazia	KU892553	KU853799	-	-	Bianchi et al. 2016
Ladeaschistus bilobus (Stål)	KU892554	KU853800	KU853779	KU853762	Rolston 1973
Ladeaschistus borgesi Bianchi, Cioato and Grazia	KU892555	-	KU853780		Cioato et al. 2015
Mitripus acutus Dallas	KU892547	KU853793	KU853774	KU853758	Bianchi et al. 2017b
Mitripus convergens (Herrich-Schäffer)	KU892548	KU853794	-	-	Bianchi et al. 2017b
Mitripus seclusus sp. n. Bianchi, Krein, Rider and Grazia	-	-	-	-	
Mitripus bovillus (Distant) comb. n.	-	-	-	-	Distant 1900
Padaeus viduus (Vollenhoven)	-	-	-	-	Vollenhoven 1868
Sibaria amazonica Krein, Rider and Grazia	-	-	-	-	Krein et al. 2020
Sibaria armata (Dallas)	KU892556	KU853801	KU853781	KU853763	Krein et al. 2020
Sibaria englemani Rolston	KU892557	-	KU853782	-	Krein et al. 2020

and also genitalic structures of the both sexes were taken in sequential focus using a Nikon AZ100M and digitally stacked in the NIS Elements software, available in the Zoology Department of Universidade Federal do Rio Grande do Sul.

The specimens used for this study were borrowed from: DARC: David A. Rider Collection, Department of Entomology, North Dakota State University, Fargo, North Dakota; UFRG: Coleção do Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; Joseph E. Eger personal collection (JEEC) USNM: National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; and NHMUK: The Natural History Museum, London, United Kingdom.

RESULTS

TAXONOMY

(The taxonomies in this section are based on the phylogenetic analyses. See below)

Pentatomidae Leach, 1815

Pentatominae Leach, 1815
Genus *Mitripus* Rolston, 1978

Mitripus seclusus sp. n. Bianchi, Krein, Rider and Grazia

(Figs. 1–5, Table 3)

urn:lsid:zoobank.org:act:ECBED1B6-EC60-440D-A826-89322D5F6674

Type Material: Holotype: ECUADOR: 1 male, Paramba, Ecuador / Coll. I. R. Sc. N. B, Equateur: Paramba, Ecuador (UFRG); 1 female, Paramba, Ecuador / Collection Rosenberg / NMNH.

Etymology: The name is allusive to the seclusion among the authors while describing this species (L. *seclusus*: shut up, separated, recluse, seclude). Most of the intellectual work was made during the pandemic of COVID-19, with the authors respecting proper social distancing.

Diagnosis: *Mitripus seclusus* sp. n. may be distinguished from *M. convergens* and *M. legionarius* by each humeral angle developed laterally as a stout spine; from *M. acutus* by the clypeus being slightly longer than the mandibular plates, and the anterolateral margins of the pronotum entirely smooth; and from *M.*

Table 2. Morphological partition based on Bianchi et al. (2017b). Character state matrix for the phylogenetic analysis of *Mitripus bovillus* (Distant) and related carpocorines. Taxa in bold are not present in Bianchi et al. (2017b). -. inapplicable data; ?. missing data

Adustonotus grandis	1001100000111111213120001 00-11111101010010101000000001110001011101020001001-111111?-11
Adustonotus hansi	1000101000010111210010011 00-11111000110010121000000002010201211000-40001001-1011111-11
Adustonotus saramagoi	1001100001010111210010011 00-11112110010010121000000001010201211001040001001-1310111211
Adustontous paranticus	1000100000011111210001011 00-11111101110010101001000000010201011100-40001001-131011?-11
Agroecus scabricornis	1201100000101211221010101 00-0010011000-1100000???001000???11210101000111101-1110100?10
Caonabo pseudoscylax	1011101111001210-2101000000-1101311001002100101?11000002100001011 0?20200-0001031111010
Diceraeus furcatus	1120101000011101001121001 00-0000110011000110111001011001100011012101000 1101-1011110-11
Dichelops (*D.*) *leucostigmus*	1120100111101111021010001 00-0101111010-0111000???11100010200110121130001101-112111??01
Euschistus (*E.*) *crenator*	2210101001011001021011101 00-0100210010-0201001101000000000001211110-3010110011200110-00
Euschistus (*E.*) *heros*	2210101101011101021120101 00-0100311110-0200201101102010100000010110-1010111011211110-01
Euschistus (*E.*) *taurulus*	0210101010111001221020101 00-0100110000-0211200100002010201000000110-2010110011211110-00
Euschistus (*L.*) *circumfusus*	0210000010011001122001001010010?0110110010011110100101010011000111030111110112211112 11
Euschistus (*L.*) *cornutus*	0110101110010101223020111 00-0011011001100101110010020103001121011101011111011221111211
Euschistus (*L.*) *triangulator*	2211101110011001221020101110001101100110010211101102010300112001110201111001122111211 1
Glyphepomis spinosa	2110111101010100-2102000000-1001011100-0110000000001010300001101 10?100110000100011-?00
Ladeaschistus bilobus	1210000010111011?2001100100-1110210011012012100200000101120001000102100 1001-10100?0-11
Ladeaschistus borgesi	0200100000111111221001011010111020001101200210020000010112000100010310010 01-11110?0?11
Mitripus acutus	2201000000011011221011001010111010011100200010010001020112010011 00-30001001-1211100-11
***Mitripus bovillus* comb.n.**	**1200000000111010?2111100101011102100110020001001010100011200001001150001001?1301110?01**
Mitripus convergens	0000101000111011210001001010111010010100201210010000020112000101 00-30001001-111111?-11
***Mitripus seclusus* sp. n.**	**1200000000111010?2101100101011102100110020001001010?????000010011500?1001-1301110-01**
Padaeus viduus	**2010000100100111021010001010001130101110101000010100100200001111 10?00101100?1221101201**
Sibaria amazonica	**0201101001111211121011101010111021001101100010000100000112000001010300010 01-111111-?01**
Sibaria armata	0201000001111311121011001010111010001101100210000100000112000101010400010 01-111111-?01
Sibaria englemani	0200000001111311121011101010111000001101200010000100000112000101010300010 01-111111-?01

bovillus by the humeral angles not depressed anteriorly, and by the shape of the parameres (Fig. 3).

Description: *Coloration*: Dorsal surface ochraceous with black punctures, giving an overall dark brown matte aspect; antennae ochraceous ventrally and basally, brownish dorsally. Scutellum darker basally than apically. Connexivum brownish, middle third ochraceous. Ventral surface yellowish ochraceous; head and abdomen impunctate, thorax with brownish-yellow punctures. Legs ochraceous with reddish-brown spots on femora and tibiae; each femur with brownish ring at apex; apex of each tarsomere brownish.

Head: Clypeus slightly longer than mandibular plates, both rounded apically. Head tapering to apex, lateral margins of mandibular plates sinuous, concave near eyes. Ocelli red or yellow. Antennomere

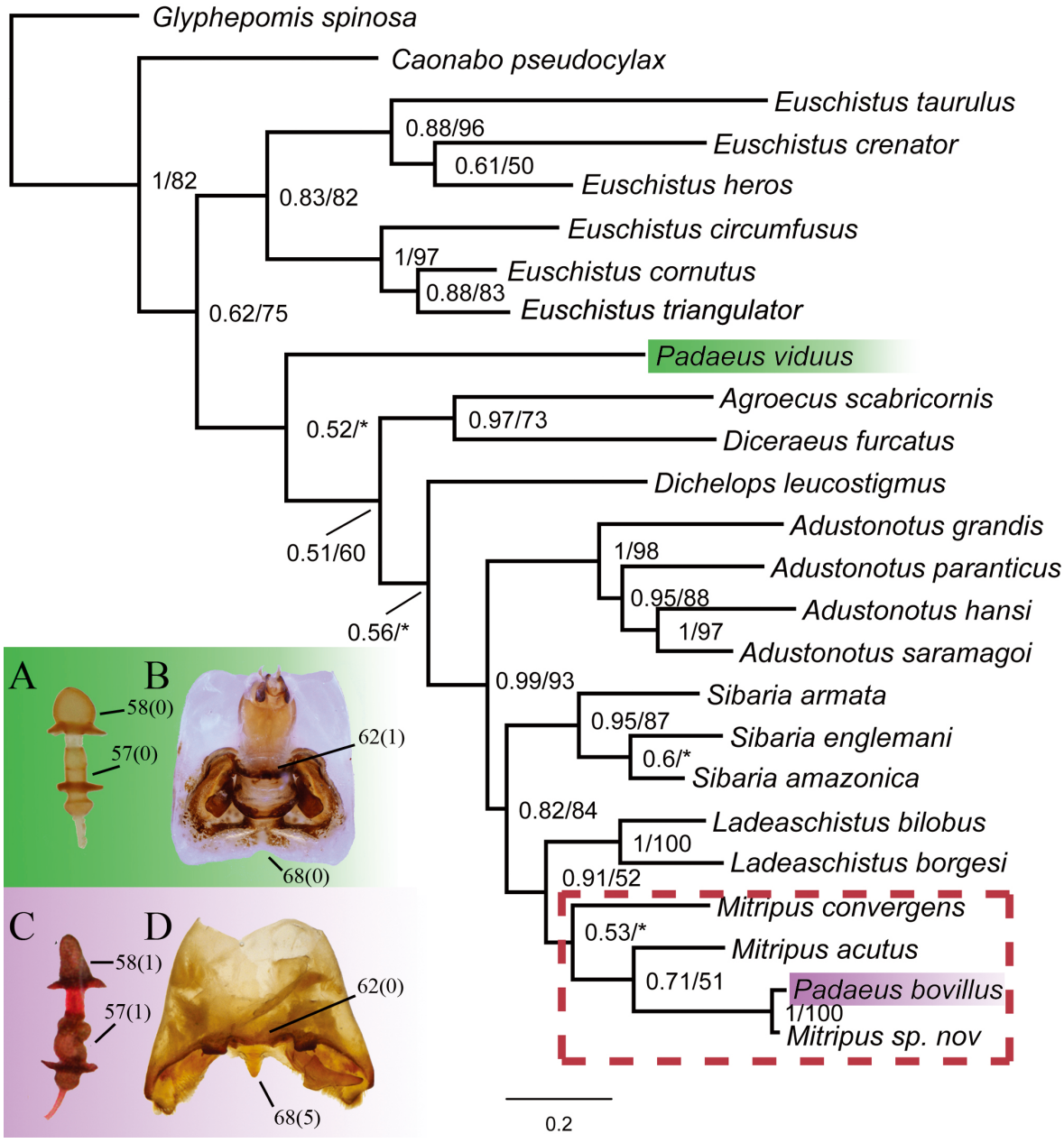

Fig. 1. Bayesian Inference consensus tree based on the analysis of four molecular markers and morphological characters from 25 species of carpocorines. Numbers close to nodes are Bayesian posterior probability / Maximum-Likelihood bootstrap support, respectively. Only nodal support above PP = 0.5 or BS = 50 were collapsed ("*" indicates uninformed value); A–B, *Padaeus viduus* (Vollenhoven); C–D, *Mitripus bovillus* comb. n. (Distant): A: *capsula seminalis*; B: pygophore; C: *capsula seminalis*; D: pygophore (numbers near to the genitalic structures indicate character and state); red dashed line delimitates *Mitripus* clade.

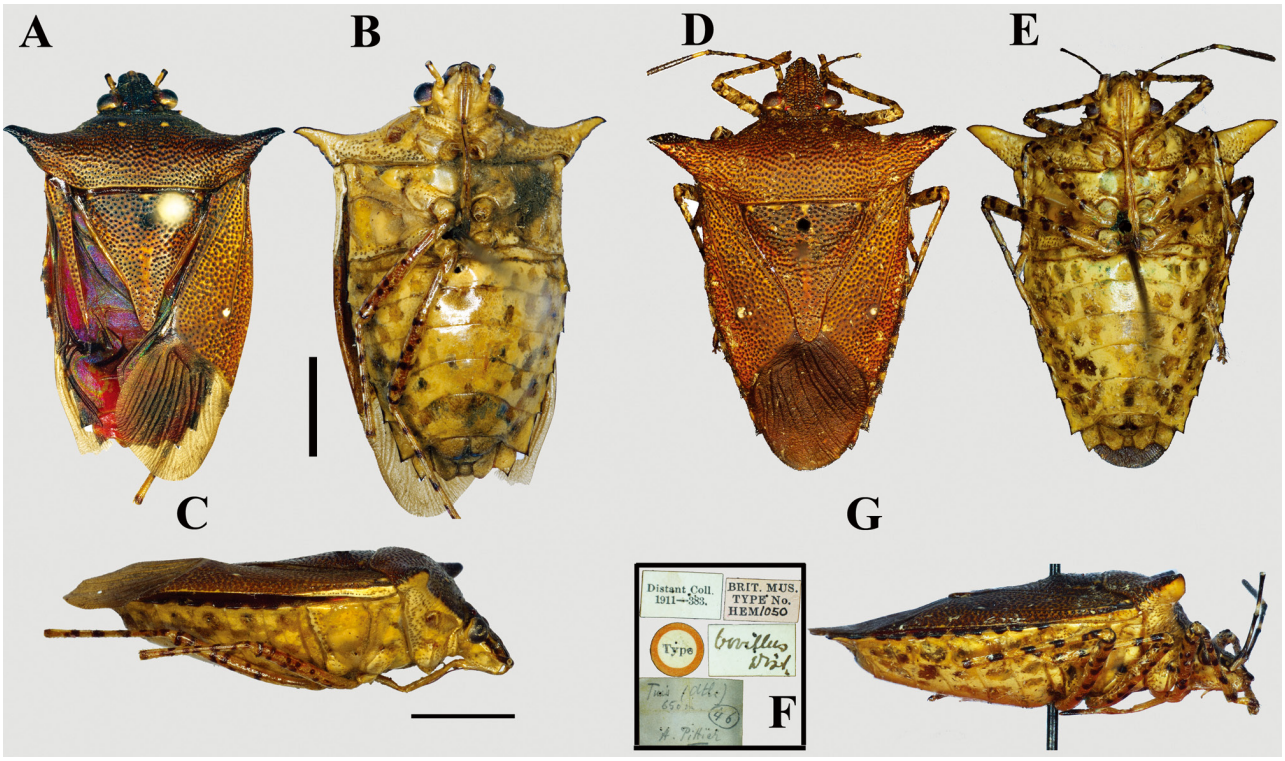

Fig. 2. Habitus of *Mitripus seclusus* and *Mitripus bovillus.* A–C, *Mitripus seclusus* sp. n.: A: dorsal; B: ventral; C: lateral; D–G, *Mitripus bovillus* comb. n. (Distant): D: dorsal; E: ventral; F: labels; G: lateral. Scale bars = 1 mm.

Table 3. Measurements: mean (± standard deviation) given in millimeters of morphometric parameters of *Mitripus bovillus* comb. n. (Distant) and *Mitripus seclusus* sp. n.

	Mitripus bovillus comb. n.		*Mitripus seclusus* sp. n.	
	Male (n = 3)	Female (n = 3)	Male (n = 1)	Female (n = 1)
BL	10.93 (0.35)	11.60 (0.66)	10.00	9.90
AW	5.53 (0.15)	6.07 (0.31)	5.00	5.40
HL	2.00 (0.00)	2.13 (0.06)	1.80	1.60
HW	2.30 (0.10)	2.40 (0.10)	2.10	2.10
LE	1.10 (0.10)	1.13 (0.06)	1.00	0.80
ID	0.97 (0.06)	1.03 (0.15)	1.00	1.00
I	0.60 (0.00)	0.67 (0.06)	0.50	0.50
II	1.17 (0.06)	1.20 (0.00)	1.00	-
III	1.33 (0.06)	1.47 (0.06)	1.20	-
IV	1.90 (0.00)	2.25 (0.07)	-	-
V	1.95 (0.07)	2.10	-	-
PL	2.43 (0.06)	2.70 (0.10)	2.30	2.20
PW	8.50 (0.36)	8.87 (0.45)	7.60	7.60
SL	3.80 (0.20)	4.00 (0.35)	3.60	3.70
SW	3.57 (0.06)	3.90 (0.26)	3.30	3.60

BL: total body length; AW: abdominal width; HL: head length; HW: head maximum width; LE: length of head before eyes; ID: interocular distance; I; II; III; IV; V: antennomere length I, II, III, IV, V respectively; PL: pronotal length; PW: pronotal maximum width; SL: scutellar length; SW: scutellar maximum width.

Fig. 3. Male genitalic structures of *Mitripus seclusus* sp. n. and *Mitripus bovillus* comb. n. (Distant). A–J, *Mitripus seclusus*: A–C: pygophore: A: dorsal view; B: posterior view; C: ventral view; D–G: left paramere: D: dorsal view; E: ventral view; F: lateral view; G: mesial view; H–J: phallus: H: ventral view; I: lateral view; J: dorsal view; K–T, *Mitripus bovillus*: K–M: pygophore: K: dorsal view; L: posterior view; M: ventral view; N–Q: left paramere: N: dorsal view; O: ventral view; P: lateral view; P: mesial view; R–T: phallus: R: ventral view; S: lateral view; T: dorsal view. App: apical process of paramere, bpp: basal process of paramere, dr: dorsal rim, spdr: superior process of dorsal rim, tr: transverse ridge, vr: ventral rim. Scale bars = 1 mm.

proportions: I < II < III (IV and V lacking). Anterior margins of bucculae truncate with sharp projections, posterior margins evanescent. Gena flat. Rostrum reaching anterior margins of metacoxae.

Thorax: Anterolateral margin of pronotum smooth on anterior half, slightly sinuous; anterolateral angles developed as small yellowish-ochraceous spines, projected laterally. Each humeral angle produced laterally as a black stout spine. Pronotal cicatrices brownish, with an ochraceous spot posterior to each mesial angle. Basal angles of scutellum with small foveae. Apex of radial vein with a small ivory dot at endocorium. Membrane of hemelytra fumose, with subparallel veins. Evaporatoria each extending halfway from ostiole to metapleural lateral margin; surface impunctate, presenting gyrification near ostioles; lateral fold present; peritreme spout-like.

Abdomen: Each posterolateral angle of connexiva developed as a tiny black spine. Posterolateral angles of urosternite VII slightly projected as a spine. Spiracles concolorous with abdominal disc.

Male genitalia: Pygophore (Fig. 3A–C): In dorsal view, trapezoidal; genital cup not well exposed; each posterolateral angle of pygophore projected as a small triangle, rounded apically; median projection of dorsal rim short. Dorsal rim interrupted by diagonal depressions flanking median projection of dorsal rim; lateral margins slightly sinuous, discontinuous near median projection of dorsal rim; superior process of dorsal rim exposed, rectangular; ventral rim concave with a triangular projection at middle. In posterior view, genial cup opening ellipsoid; dorsal rim concave, smooth; superior process of dorsal rim long, blade-like; transverse ridge concave medially, U-shaped; inferior layer of ventral rim medially straight, tumescent laterally. In ventral view, ventral rim concave with a triangular projection at middle; posterolateral angles projected posteriorly, slightly bifid. Tenth segment: posterior margin trapezoidal with setae; disc smooth; tubercles on basal third slightly developed. Parameres (Fig. 3D–G): In dorsal and ventral view: each with basal apodeme smaller than crown; stem slightly smaller than crown; crown bending outward nearly at a 45° angle. Basal process of paramere narrow, rounded, with long setae; apical process of paramere enlarged basally, tapering towards truncate apex. In mesial and lateral views: apical process of paramere stout, triangular, with scale-like structures on its outer surface. Phallus (Fig. 3H–J): Phallotheca tubular, slightly constricted basally; ventral basal processes of phallotheca quadrangular; dorsal processes of phallotheca hook-like, bent ventrally in about 45°, short, not surpassing expanded conjunctiva; vesica process spout-like; conjunctiva lacking processes; *ductus seminis distalis* short, not exposed out of phallotheca.

Female genitalia: In posteroventral view (Fig. 4A), gonocoxites VIII with shallow punctures, concolorous with ochraceous disc; surface flat with a slightly depressed area near posterolateral margin; mesial margins straight, overlapping, with a brown spot apically; apex squared. Laterotergites VIII with black margins; apex spine-like. Gonocoxites IX trapezoid, about three times wider than long, anterior and lateral margins straight, posterior margin concave. Laterotergites IX rounded apically, mesial margins forming a right angle, lateral margins convex, slightly surpassing tergite VIII; segment X rectangular.

Distribution: *Mitripus seclusus* sp. n. is known only from Ecuador (Fig. 5).

Pentatomidae Leach, 1815
Pentatominae Leach, 1815
Genus *Mitripus* Rolston, 1978

Mitripus bovillus (Distant) comb. n.

(Figs. 1–5, Table 3)

urn:lsid:zoobank.org:act:6910E7CD-BB6F-4222-A9E2-F2E155BE3C59

Padaeus bovillus Distant, 1900: 689, 690 (original description); Kirkaldy, 1909: 69 (catalog); Rolston, 1976: 7 (revision).

Material examined: Type Material: Holotype female: COSTA RICA: Tuis, Cartago, Terralba 650 m., A. Pittier, BRIT. MUS. (NHMUK) TYPE HEM/050. COSTA RICA: 1m#, Costa Rica, Prov. Heredia, F. La Selva, 3km S Pto. Viejo, 10°26'N 84°01'W / 25.III.1987, H. A. Hespenheide / D. A. Rider Collection (DARC); 1f#, Costa Rica, Pr. Heredia, Puerto Viejo, Finca La Selva / R J. Marquis, coll. No. I, 11.IX.1986 / *Piper aricianum* (?) / NMNH; 1f#, Collection Schild-Burgdorf, Costa Rica, San Carlos / *Padaeus bovillus* Distant / NMNH ; 1m# / Costa Rica: Cartago Prov., Mon. Nac. Guayabo, 22.XII.1994 / M. J. Tauber, C. A. Tauber, P. J. Tauber Collectors / UC Berkeley EMEC 1240641. PANAMA: 1m#, 1f#, Panama: Bocas Del Toro Pr. 3km. n. Continental Div. on Fortuna Hwy 925 m., 13.VII.1996, A. R. Gillogly / EGER / *Sibaria* n. sp. Det. J. E. Eger, 1997 (UFRG).

Diagnosis: *Mitripus bovillus* may be distinguished from *M. convergens* and *M. legionarius* by the humeral angles which are developed laterally as stout spines; from *Mitripus acutus* by the clypeus slightly longer than mandibular plates, anterolateral margins of pronotum entirely smooth; and from *Mitripus seclusus* by the humeral angles depressed anteriorly and the shape of parameres (Fig. 3).

Redescription: *Coloration*: Dorsal surface ochraceous with black punctures, giving an overall dark

brown matte aspect; head and thorax with ochraceous punctures; antennae ochraceous, antennomeres I–II with irregular dark brown spots, antennomeres III–IV dark on apical 3/4, and antennomere V dark brown on apical half. Scutellum dark brown on base. Connexivum blackish, middle third ochraceous. Ventral surface yellowish-ochraceous; abdomen impunctate. Legs ochraceous with brown spots on femora and tibiae; apex of each tarsomere brownish.

Head: Clypeus slightly longer than mandibular plates, rounded apically. Head tapering to apex, lateral margins of mandibular plates sinuous, concave near eyes. Ocelli red or yellow. Antennomere proportions: I < II < III < IV = V. Anterior margins of bucculae truncated, each with sharp projection, posterior margins evanescent. Rostrum reaching metacoxae.

Thorax: Anterolateral margins of pronotum smooth on anterior half, anterolateral angles developed as small yellowish-ochraceous spines, projected laterally. Each humeral angle produced laterally as a black, stout spine, somewhat depressed anteriorly. Pronotal cicatrices brownish, with ochraceous spot posterior to mesial angles. Basal angles of scutellum with small fovea. Apex of radial vein with a small ivory dot at endocorium. Hemelytral membrane fumose, with veins subparallel. Evaporatoria each extending halfway from ostiole to metapleural lateral margin, and present on posterior margin of mesopleuron; surface impunctate, with gyrification near ostiole; lateral fold present; peritreme spout-like.

Abdomen: Posterolateral angles of connexiva developed as tiny black spines. Posterolateral angles of urosternite VII slightly projected as spines. Spiracles concolorous with abdominal disc.

Male genitalia: Pygophore (Fig. 3K–M): in dorsal view, pygophore trapezoidal; genital cup not well exposed; posterolateral angles of pygophore developed as rounded projections; median projection of dorsal rim short. Dorsal rim interrupted by diagonal depressions flanking median projection of dorsal rim, lateral

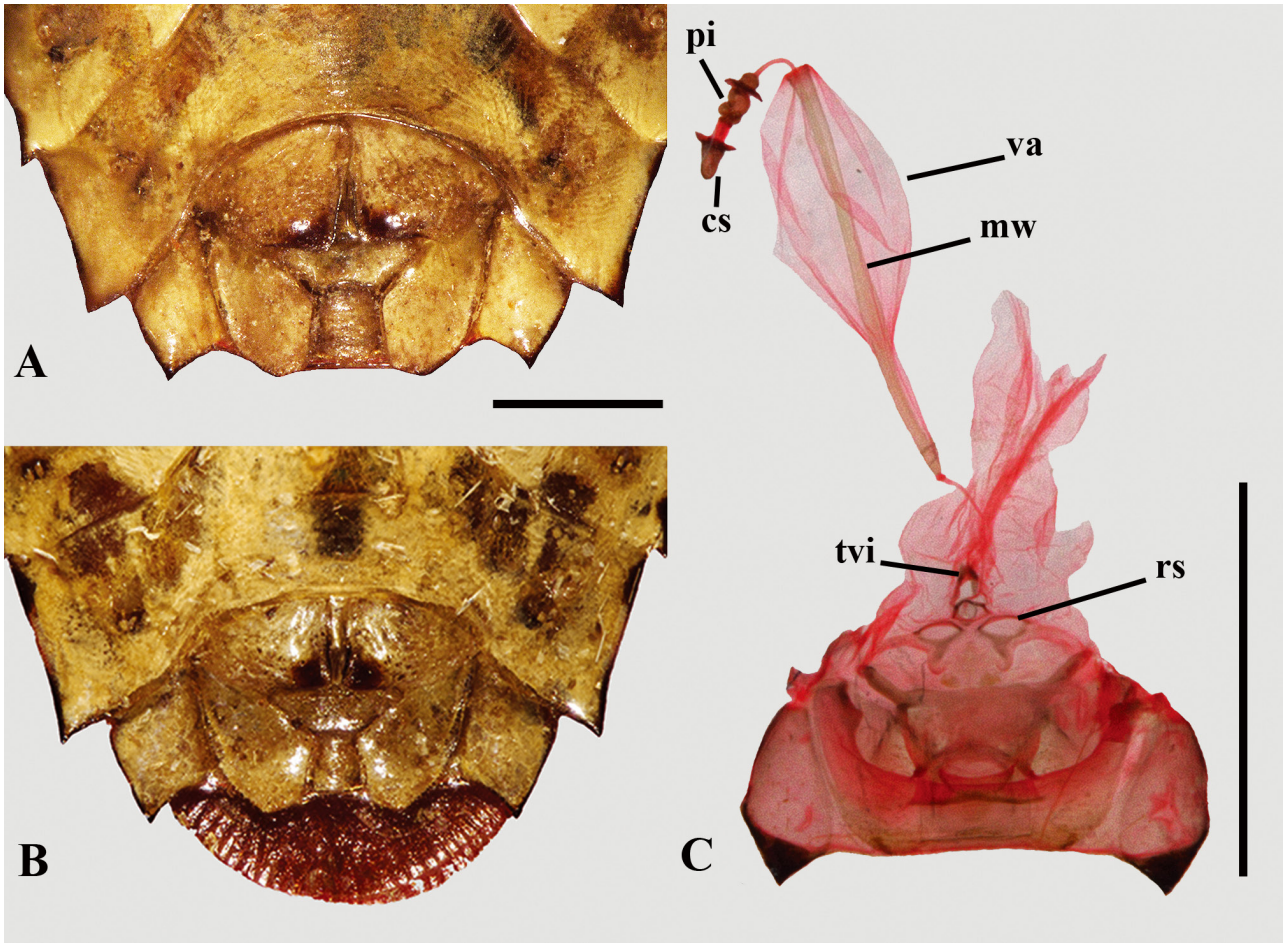

Fig. 4. Female genitalic structures. A: *Mitripus seclusus* sp. n.; B–C *Mitripus bovillus* comb. n. (Distant). A–B: posteroventral view of female terminal abdominal segments; C: internal genitalic structures. cs: *capsula seminalis*, mw: median wall, pi: *pars intermedialis*, rs: ring sclerites, tvi: thickening of vaginal intima, va: vesicular area. Scale bars: 1 mm.

margins slightly sinuous, discontinuous near median projection of dorsal rim; superior process of dorsal rim exposed. Transverse ridge slightly concave; ventral rim concave with triangular projection medially. In posterior view, genital cup opening ellipsoid; dorsal rim concave, smooth; superior process of dorsal rim truncate, blade-like.; transverse ridge concave medially, U-shaped; inferior layer of ventral rim tumescent laterally, medial triangular projection bent inward into genital cup. In ventral view, ventral rim biconcave, triangular projection medially; posterolateral angles produced, rounded. Tenth segment: Posterior margin trapezoidal with setae; disc smooth; tubercles on basal third slightly developed. Parameres (Fig. 3N–Q): In dorsal and ventral views, each with basal apodeme smaller than crown; stem as long as crown; crown bending outward nearly at a 45° angle. Basal process of paramere not developed, with a few setae; apical process of paramere enlarged basally, tapering to truncate apex. In mesial and lateral views, apical process of paramere stout, triangular, with scale-like structures on its outer surface. Phallus (Fig. 3 R–T): phallotheca tubular, slightly constricted basally; ventral basal processes of phallotheca quadrangular; dorsal processes of phallotheca hook-like, bent ventrally in about a right angle, not surpassing expanded conjunctiva; vesica process spout-like; conjunctiva lacking processes; *ductus seminis distalis* short, not exposed out of phallotheca.

Female genitalia: In posteroventral view (Fig. 4B), gonocoxites VIII with shallow punctures concolorous with ochraceous disc; surface flat; mesial margins concave, exposing a scletorized area of gonapophyses VIII, apex of each mesial margin squared, with brown spot. Laterotergites VIII with black margins; apex of each developed as a spine. Gonocoxites IX trapezoid, about three times wider than long, anterior, posterior

Fig. 5. Distribution records of *Mitripus seclusus* sp. n. and *Mitripus bovillus* comb. n. (Distant).

and lateral margins straight. Laterotergites IX rounded apically, mesial margins forming a right angle, lateral margins convex, posterior margins projected, slightly surpassing tergite VIII; segment X rectangular. Internal genitalia: Ring sclerites elliptical; thickening of vaginal intima triangular posteriorly, rounded anteriorly; *ductus receptaculi* proximally slightly enlarged near vesicular area, shorter than vesicular area; median wall of vesicular area straight, slightly enlarged at apex; *ductus receptaculi* distally straight, shorter than *pars intermedialis*, with rounded dilation apically; proximal and distal annular flanges convergent; *pars intermedialis* convoluted, sclerotized basally, apical half straight, membranous; *capsula seminalis* thumb-like, dilated anteriorly.

Distribution: *Mitripus bovillus* is distributed throughout southern Central America, with records from Costa Rica and Panama (Fig. 5).

Comments: Distant (1900) originally speculated that *Padaeus bovillus* resembled *Sibaria armata*. More recently, Rolston (1976) called attention to the "arcuately truncate termination of the bucculae well before the distal end of the first rostral segment" that should remove *P. bovillus* from *Padaeus* and suggested that the species was close to *Mormidea*, and that further investigation was needed. A phylogenetic hypothesis previously placed *Padaeus* within *Euschistus* group, close to *Proxys* Spinola, although *Padaeus bovillus* was not sampled (Barão et al. 2020).

Phylogenetic analyses

The phylogenetic trees (Fig. 1) were built based on 2,416 characters (*i.e.*, 86 morphological; 16S 531 bp 28S 528 bp COI 818 bp Cytb 453 bp). The phylogenies under BI and ML recovered similar topology (Fig. 1). The close relationship between *M. bovillus* comb. n. and *M. seclusus* sp. n. (see below the taxonomic acts) was highly supported (PP = 1; BS = 100). The analyses resulted in *M. bovillus* and *M. seclusus* being more related to other *Mitripus* species than to *P. viduus* and the other sampled taxa. *Mitripus acutus* was recovered as sister to *M. bovillus* and *M. seclusus* with moderate values (PP = 0.71; but low value under ML, BS = 51), and *Mitripus* highly supported as sister to *Ladeaschistus* (PP = 0.91; but moderate value under ML, BS = 51).

Padaeus here represented by its type species (*i.e.*, *P. viduus*) was distantly related to *Mitripus*, which is included in the highly supported clade *Adustonotus* (*Sibaria* (*Ladeaschistus*; *Mitripus*)) (PP = 0.99; BS = 93). *Padaeus viduus* was more closely related to *Euschistus* and *Caonabo*. Our phylogenetic hypothesis also allowed us to test the placement of *S. amazonica* within *Sibaria*, since this species was recently described lacking phylogenetic evidence; the monophyly of *Sibaria* was recovered (PP = 0.95; BS = 87).

DISCUSSION

In this paper, we tested for the first time the phylogenetic position of *Padaeus bovillus*. For this, we used a total evidence phylogenetic approach based on molecular and morphological data. Based on the results, we proposed *Mitripus bovillus* comb. n. and describe its sister species *M. seclusus* sp. n.

Our analyses recovered a monophyly of *Mitripus* with low support (PP = 0.53). However, the hypothesis of *Mitripus* as monophyletic was strongly supported in a recent study using a comprehensive sample of taxa related to *Mitripus* (Bianchi et al. 2017b). The complete lack of molecular data for some taxa (see Table 1) likely negatively affects the support for the tree, *e.g.*, *Mitripus*. The non-random distribution of missing data can provide a radical instability to the node-support values (Simmons 2012; Xi et al. 2016). Although there was low support for a few nodes in the analyses, our results are indubitable concerning the position of *M. bovillus*.

The first phylogenetic hypothesis suggesting the non-monophyly of *Euschistus* and a close relationship between *Euschistus* (*Mitripus*)—currently *Adustonotus* and *Mitripus*—and *Ladeaschistus* was a cladistic analysis based on morphological characters (Weiler et al. 2016). The complete sampling of *Euschistus* (*Mitripus*), *Ladeaschistus* and *Sibaria* using morphological and molecular data inferred these taxa to be a clade more closely related to other Carpocorini genera (*i.e.*, *Dichelops*, *Diceraeus* Dallas, and *Agroecus* Dallas) than to *Euschistus* (Bianchi et al. 2017b). More recently, Barão et al. (2020) tested the *Euschistus* group using morphological characters and also recovered the relationship among *Adustonotus*, *Ladeaschistus*, and *Mitripus*. In this analysis species of *Sibaria* were not sampled.

The intricate taxonomic history of these four genera date back to Rolston (1973), who described *Ladeaschistus* to include some species of *Euschistus* that were notably different from their congeners. These species present conspicuous male and female genitalia characters (*e.g.*, superior ridge of the pygophore tectiform, parameres bent inversely, *capsula seminalis* finger-like) and armed femora. Rolston (1973) also analyzed other species of *Euschistus* (*i.e.*, *Euschistus tristigmus* and *Mitripus acutus*, cited as *Euschistus anticus*), and suggested affinity between *Ladeaschistus* and a South American group of *Euschistus*, represented by *M. anticus*. An equivalent pattern of female genitalia was found in *Sibaria* (Rolston 1975), and moreover,

Sibaria species have armed femora. Armed femora are a peculiar feature present in a few Carpocorini (*e.g.*, *Agroecus*, *Mathiolus* Distant, *Spinalanx* Rolston and Rider). Then, a putative close relationship was presumed between *Ladeaschistus* and *Sibaria* (Rolston 1975). *Mitripus* was proposed by Rolston (1978) to be a subgenus of *Euschistus*. However, Rolston (1978) hinted at the plausible affinity among *E.* (*Mitripus*), *Ladeaschistus*, and *Sibaria*. Before the systematic proposition of Bianchi et al. (2017b), the subgenus included 11 species (Cioato et al. 2015). Bianchi et al. (2017b) raised *Mitripus* to the generic rank, with three species, and described *Adustonotus* to include the other eight species previously placed in *Mitripus*. Considering our results and the taxonomic decisions contained herein, *Mitripus* should now also include *M. bovillus* and *M. seclusus*, thus raising the number of species to five.

Padaeus viduus, the type species of *Padaeus*, was recovered as phylogenetically distant from *M. bovillus*. Indeed, doubts around the placement of *M. bovillus* in *Padaeus* (Rolston 1976; Rolston and McDonald 1984) present a new hypothetical scenario concerning the relationships within *Euschistus* group. The lobed posterior margins of the bucculae have been used as the main character separating *Padaeus* from those genera included in *Euschistus* group (Rolston 1974a). *Mitripus bovillus* has the posterior margins of the bucculae evanescent, similar for example to *Mitripus*, *Sibaria* and *Euschistus* (for some additional different states of genitalic characters between *P. viduus* and *M. bovillus*, see Fig. 1A–D). Other features present in *Mitripus* and different in *P. viduus* are: rostrum short, not surpassing the metacoxae (character 14(state - 0)); humeral angles of pronotum oriented laterally (22(1)); mesial margins of gonocoxites VIII overlapping basally (45(1)); *capsula seminalis* finger-like (58(2)); and *ductus seminis distalis* shorter than phallothecal diameter (75(1)).

Sibaria amazonica was recently described in a review of the genus *Sibaria* (Krein et al. 2020). The authors based its taxonomic position only on morphological features, without a hypothesis supported by a phylogenetic analysis. Our phylogenetic hypothesis corroborates the placement of *S. amazonica* in this genus (Krein et al. 2020), and also its monophyly (Bianchi et al. 2017b). The intraspecific morphological variations overlap interspecific variations, making the external morphology of *Sibaria* difficult for specific identification. Krein et al. (2020) inferred similarity between the male genitalia of *S. amazonica* and *S. andicola* Breddin. For now, we think that any relationship among species within *Sibaria* is speculative at best because our sample lacks *S. andicola*, and the support for *S. amazoniza* and *S. englemani* is low (PP = 0.6).

CONCLUSIONS

Herein, we hypothesize the taxonomic placement for *Mitripus bovillus* comb. n. and *Mitripus seclusus* sp. n. based on the results of phylogenetic methods. The type species of *Padaeus* was more closely related to *Caonabo* and *Euschistus* than to *M. bovillus*. We argue that the use of phylogenetic frameworks is desirable for the classification of taxonomic units within the Pentatomidae, and hypotheses based on this method should be used as often as possible by the researchers.

Acknowledgments: This work and the new species names were registered with ZooBank under urn:lsid:zoobank.org:pub:EE3FD306-0E71-4984-8275-B023D04F4142. We are thankful to the curators of the listed collections, who loaned the specimens for this study; Victor Carabajal for the *Padaeus viduus* pictures; Valentina Castro-Huertas for the critical reading of the final draft; and Joseph Eger and Gimena Dellape for their valuable contributions. Financial support from Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (Ed. Universal Proc. 400599/2016-3), and CNPq fellowships to J.G. (Proc. 305009/2015-0) and V.K. (Proc. 168812/2017-7). Also to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—CAPES for postdoc fellowships to F.M.B.—Finance Code 01.

Authors' contributions: FMB designed the paper, (re)described the species, executed the phylogenetic analyses, drafted the manuscript and wrote results and discussions. VK took pictures and (re)described the species. All authors contributed to drafting and revising the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interests.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Baker AD. 1931. A study of the male genitalia of Canadian species of Pentatomidae. Can J Res **4:**148–220. doi:10.1139/cjr31-013.

Barão KR, Ferrari A, Grazia J. 2020. Phylogenetic analysis of

the *Euschistus* group (Hemiptera: Pentatomidae) suggests polyphyly of *Dichelops* Spinola, 1837 with the erection of *Diceraeus* Dallas, 1851, stat. rev. Austral Entomol **59:**770–783. doi:10.1111/aen.12489.

Bianchi FM, Gonçalves VDR, de Souza JR, Campos LA. 2016. Description of three new species of *Glyphepomis* Berg (Heteroptera: Pentatomidae: Pentatominae). Zootaxa **4103:**443–452. doi:10.11646/zootaxa.4103.5.2.

Bianchi FM, Barão KR, Grazia J. 2017a. Review of the sulcacitus group of *Euschistus* (Pentatomidae: Pentatominae: Carpocorini) with description of the internal female genitalia and a new species. Zootaxa **4362:**348–358. doi:10.11646/zootaxa.4362.3.2.

Bianchi FM, Deprá M, Ferrari A, Grazia J, Valente VLS, Campos LA. 2017b. Total evidence phylogenetic analysis and reclassification of *Euschistus* Dallas within Carpocorini (Hemiptera: Pentatomidae: Pentatominae). Syst Entomol **42:**399–409. doi:10.1111/syen.12224.

Cioato A, Bianchi FM, Eger J, Grazia J. 2015. New species of *Euschistus* (*Euschistus*) from Jamaica, *Euschistus* (*Mitripus*) and *Ladeaschistus* from southern South America (Hemiptera: Heteroptera: Pentatomidae: Pentatominae). Zootaxa **4048:**565–574. doi:10.11646/zootaxa.4048.4.7.

Distant WL. 1900. Contributions to a Knowledge of the Rynchota II. Rhynchota Central America. Trans Entomol Soc Lond **1900:**687–695.

Dupuis C. 1970. Heteroptera. *In*: Tuxen SL (ed.) Taxonomist's glossary of genitalia of insects. Munskgaard, Copenhagen. doi:10.4039/ent103144-1.

Grazia J, Schuh RT, Wheeler WC. 2008. Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). Cladistics **24:**932–976. doi:10.1111/j.1096-0031.2008.00224.x.

Henry TJ. 1997. Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. Ann Entomol Soc Am **90:**275–301. doi:10.1093/aesa/90.3.275.

Hickmann F, Moraes T, Bianchi FM, Correa AS, Schwertner CF. 2019. Integrating data to redescribe *Euschistus taurulus* Berg (Hemiptera: Pentatomidae). Zootaxa **4688:**119–134. doi:10.11646/zootaxa.4688.1.7.

Kirkaldy GW. 1909. Catalogue of Hemiptera (Heteroptera). Cimicidae, vol 1, Berlin, Germany. doi:10.5962/bhl.title.15205.

Kment P, Vilímová J. 2010. Thoracic scent efferent system of Pentatomoidea (Hemiptera: Heteroptera): a review of terminology. Zootaxa **2706:**1–77. doi:10.11646/zootaxa.2706.1.1.

Krein V, Bianchi FM, Rider DA, Grazia J. 2020. Taxonomic review of *Sibaria* Stål, 1872 (Heteroptera: Pentatomidae: Pentatominae: Carpocorini), with description of a new species. Zootaxa **4779:**391–408. doi:10.11646/zootaxa.4779.3.7.

Lewis PO. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst Biol **50:**913–925. doi:10.1080/106351501753462876.

Li HM, Deng RQ, Wang JW, Chen ZY, Jia FL, Wang XZ. 2005. A preliminary phylogeny of the Pentatomomorpha (Hemiptera: Heteroptera) based on nuclear 18S rDNA and mitochondrial DNA sequences. Mol Phylogenetics Evol **37:**313–326. doi:10.1016/j.ympev.2005.07.013.

Maddison WP, Maddison DR. 2019. Mesquite: a modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org. Accessed 22 April 2020.

Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Computer Program and Documentation Distributed by the Author [WWW document]. http://beast.bio.ed.ac.uk/Tracer. Accessed 22 April 2020.

Rider DA, Rolston LH. 1987. Review of the genus *Agroecus* Dallas, with the description of a new species (Hemiptera: Pentatomidae). J N Y Entomol Soc **95:**428–439.

Rider DA, Schwertner CF, Vilímová J, Rédei D, Kment P, Thomas DB. 2018. Higher Systematics of the Pentatomoidea. *In*: McPherson JE (ed) Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management, 1st edn. CRC Press, Boca Raton. doi:10.1201/9781315371221-2.

Rolston LH. 1973. A New South American Genus of Pentatomini (Hemiptera: Pentatomidae). J N Y Entomol Soc **81:**101–110.

Rolston LH. 1974a. Revision of the genus *Euschistus* in Middle America (Hemiptera, Pentatomidae, Pentatomini). Entomol Am **48:**1–102.

Rolston LH. 1974b. A new genus of Pentatominae from South America, distinguished by the position of its spiracles (Hemiptera: Pentatomidae). J N Y Entomol Soc **82:**57–60.

Rolston LH. 1975. A new species and review of Sibaria (Hemiptera: Pentatomidae). J N Y Entomol Soc **83:**218–225.

Rolston LH. 1976. An Evaluation of the Generic Assignment of Some American Pentatomini. J N Y Entomol Soc **84:**2–8.

Rolston LH. 1978. A new subgenus of *Euschistus* (Hemiptera: Pentatomidae). J N Y Entomol Soc **86:**102–120.

Rolston LH, McDonald FJD. 1984. A conspectus of Pentatomini of the western hemisphere. Part 3 (Hemiptera: Pentatomidae). J N Y Entomol Soc **92:**69–86.

Ronquist F, Huelsenbeck JP. 2003. MrBayes3: bayesian phylogenetic inference under mixed models. Bioinformatics **19:**1572–1574. doi:10.1093/bioinformatics/btg180.

Schaefer CW. 1977. Genital capsule of the trichophoran male (Hemiptera: Heteroptera: Geocorisae). Int J Insect Morphol Embryol **6:**277–301. doi:10.1016/0020-7322(77)90022-8.

Schuh RT, Weirauch C. 2020. True bugs of the world (Hemiptera: Heteroptera): classification and natural history (Second Edition). Siri Scientific Press, Manchester, UK.

Simmons MP. 2012. Radical instability and spurious branch support by likelihood when applied to matrices with non-random distributions of missing data. Mol Phylogenet Evol **62:**472–484. doi:10.1016/j.ympev.2011.10.017.

Stål C. 1862. Hemiptera mexicana enumeravit speciesque novas descripsit. Stett Ent Zeit **23(10/12):**437–462.

Tsai J-F, Rédei D, Yeh G-F, Yang M-M. 2011. Jewel bugs of Taiwan (Heteroptera: Scutelleridae). National Chung Hsing University, Taichung, Taiwan.

Vollenhoven SCS. 1868. Diagnosen vaneenige nieuwe soorten van Hemiptera Heteroptera. Versl Ak Amst Nat **2:**179.

Weiler LM, Ferrari A, Grazia J. 2016. Phylogeny and biogeography of the South American subgenus *Euschistus* (*Lycipta*) Stål (Heteroptera: Pentatomidae: Carpocorini). Insect Syst & Evol **47:**313–346. doi:10.1163/1876312X-47032145.

Wu YZ, Yu SS, Wang YH, Wu YH, Li XR, Men XY, Zhang YW, Rédei D, Xie Q, Bu WJ. 2016. The evolutionary position of Lestoniidae revealed by molecular autapomorphies in the secondary structure of rRNA besides phylogenetic reconstruction (Insecta: Hemiptera: Heteroptera). Zool J Linn Soc **177:**750–763. doi:10.1111/zoj.12385.

Xi Z, Liu L, Davis CC. 2016. The impact of missing data on species tree estimation. Mol Biol Evol **33:**838–860. doi:10.1093/molbev/msv266.

Supplementary materials

Table S1. List of morphological characters examined and coded for the 21 analysed terminals. (download)