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

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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...
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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), Closely, *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* Kein, 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 DNAsy 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 “-”.

<table>
<thead>
<tr>
<th>Species</th>
<th>COI</th>
<th>Cyt b</th>
<th>16S</th>
<th>28S</th>
<th>Identification literature</th>
</tr>
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<tr>
<td>Adustonotus grandis (Rolston)</td>
<td>KU892549</td>
<td>KU853795</td>
<td>KU853775</td>
<td>KU853759</td>
<td>Bianchi et al. 2017b</td>
</tr>
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<td>KU853796</td>
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<td>KU853760</td>
<td>Bianchi et al. 2017b</td>
</tr>
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<td>KU853798</td>
<td>KU853778</td>
<td>-</td>
<td>Bianchi et al. 2017b</td>
</tr>
<tr>
<td>Adustontous paranticus (Grazia)</td>
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<td>KU853797</td>
<td>KU853777</td>
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<td>Bianchi et al. 2017b</td>
</tr>
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<td>KU853783</td>
<td>KU853764</td>
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<td>Rider and Rolston 1987</td>
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<td>Caanaba pseudoscalyx (Bergroth)</td>
<td>KU892540</td>
<td>KU853784</td>
<td>KU853765</td>
<td>KU853749</td>
<td>Rolston 1974b</td>
</tr>
<tr>
<td>Diceraeus furcatus (Fabricius)</td>
<td>U892541</td>
<td>KU853785</td>
<td>KU853766</td>
<td>KU853750</td>
<td>Barão et al. 2020</td>
</tr>
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<td>Dichelops (D.) leucostigmus (Dallas)</td>
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<td>KU853786</td>
<td>KU853767</td>
<td>KU853751</td>
<td>Barão et al. 2020</td>
</tr>
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<td>KU853768</td>
<td>KU853752</td>
<td>Rolston 1974a</td>
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<td>Euschistus (E.) heros (Fabricius)</td>
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<td>KU853788</td>
<td>KU853769</td>
<td>KU853753</td>
<td>Rolston 1974a</td>
</tr>
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<td>Euschistus (E.) taurulus Berg</td>
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<td>KU853770</td>
<td>KU853754</td>
<td>Hickmann et al. 2019</td>
</tr>
<tr>
<td>Euschistus (L.) circumfusus Berg</td>
<td>-</td>
<td>KU853790</td>
<td>KU853771</td>
<td>KU853755</td>
<td>Weiler et al. 2016</td>
</tr>
<tr>
<td>Euschistus (L.) cornutus (Dallas)</td>
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<td>KU853791</td>
<td>KU853772</td>
<td>KU853756</td>
<td>Weiler et al. 2016</td>
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<td>KU853792</td>
<td>KU853773</td>
<td>KU853757</td>
<td>Weiler et al. 2016</td>
</tr>
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<td>KU853799</td>
<td>-</td>
<td>KU853755</td>
<td>Bianchi et al. 2016</td>
</tr>
<tr>
<td>Ladeaschistus bilobus (Stål)</td>
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<td>KU853800</td>
<td>KU853779</td>
<td>KU853762</td>
<td>Rolston 1973</td>
</tr>
<tr>
<td>Ladeaschistus borgesii Bianchi, Cioato and Grazia</td>
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<td>-</td>
<td>KU853780</td>
<td>-</td>
<td>Cioato et al. 2015</td>
</tr>
<tr>
<td>Mitripus acutus Dallas</td>
<td>KU892547</td>
<td>KU853793</td>
<td>KU853774</td>
<td>KU853758</td>
<td>Bianchi et al. 2017b</td>
</tr>
<tr>
<td>Mitripus convergens (Herrich-Schäffer)</td>
<td>KU892548</td>
<td>KU853794</td>
<td>-</td>
<td>-</td>
<td>Bianchi et al. 2017b</td>
</tr>
<tr>
<td>Mitripus seclusus sp. n. Bianchi, Krein, Rider and Grazia</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Distant 1900</td>
</tr>
<tr>
<td>Mitripus bovillus (Distant) comb. n.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Vollenhoven 1868</td>
</tr>
<tr>
<td>Padaeus vidus (Vollenhoven)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Krein et al. 2020</td>
</tr>
<tr>
<td>Sibaria amazonica Krein, Rider and Grazia</td>
<td>KU892556</td>
<td>KU853801</td>
<td>KU853781</td>
<td>KU853763</td>
<td>Krein et al. 2020</td>
</tr>
<tr>
<td>Sibaria armata (Dallas)</td>
<td>KU892557</td>
<td>-</td>
<td>KU853782</td>
<td>-</td>
<td>Krein et al. 2020</td>
</tr>
</tbody>
</table>
RESULTS

TAXONOMY

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

Pentatomidae Leach, 1815

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

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**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.

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

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.

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), gonoxites 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. Gonoxites 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).


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

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**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 sclerotized 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

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**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 intermedia, with rounded dilation apically; proximal and distal annular flanges convergent; pars intermedia 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 Mormideus, 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 285 528 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. vidius 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. vidius) was distantly related to Mitripus, which is included in the highly supported clade Adustonotus (Sibaria (Ladeaschistus; Mitripus)) (PP = 0.99; BS = 93). Padaeus vidius 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 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. amazonica 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.

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Henry TJ. 1997. Phylogenetic analysis of family groups within the Pentatomoidea (Hemiptera: Heteroptera): a review and coded for the 21 analysed terminals. (download)


Supplementary materials

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