Contribution to the knowledge of *Aegidinus* Arrow (Coleoptera: Scarabaeidae: Orphninae): new species and comments on the classification and nomenclature

Andrey V. Frolov\(^a\)\(^b\), Lilia A. Akhmetova\(^b\) and Fernando Z. Vaz-de-Mello\(^a\)

\(^a\)Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Brazil; \(^b\)Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia

**ABSTRACT**

Two new species of the Neotropical Orphninae genus *Aegidinus* Arrow are described: *Aegidinus noriegai* sp. nov. and *Aegidinus colbyae* sp. nov. The lectotype of *Orphnus candezei* Preudhomme de Borre is designated. *Aegidium steinheili* Harold, considered a synonym of *Aegidinus guianensis* (Westwood), is revalidated as *Aegidinus steinheili* (Harold). The following new synonymies are established: *Aegidinus oreibates* Colby, 2009 = *Aegidinus guianensis* (Westwood), syn. nov.; *Aegidinus crypticus* Colby = *Aegidinus guianensis* (Westwood), syn. nov.; *Aegidinus sunidigea* Colby = *Aegidinus candezei* (Preudhomme de Borre), syn. nov.; *Aegidinus unicus* Colby = *Aegidinus cornutus* Colby 9, syn. nov. The male of *Aegidinus simulatus* Colby is described. An updated diagnostic key to the males of *Aegidinus* is provided. The taxonomic and diagnostic characters as well as the phylogenetic relationships of *Aegidinus* are discussed.

**ARTICLE HISTORY**
Received 11 September 2018
Accepted 6 April 2019

**KEYWORDS**
scarab beetles; Aegidini; South America; teratology; genital asymmetry

**INTRODUCTION**

In the Neotropics, the scarab beetles of the subfamily Orphninae are represented by the endemic tribe Aegidiini Paulian and comprise five genera and 47 species, two-thirds of which were described in the past decade (Colby 2009; Frolov et al. 2015, 2017a, 2017b; Frolov and Vaz-de-Mello 2015; Rojkoff and Frolov 2017). *Aegidinus* Arrow is the second most speciose genus of the Aegidiini after *Aegidium* Westwood which comprises 22 species (Frolov et al. 2017a).

*Aegidinus* was recently revised by Colby (2009) who described 12 new species in addition to the three known by then. We have re-examined the types of the species described by Westwood, Harold, Preudhomme de Borre and Colby, and the results led us to revise some taxonomic decisions of previous authors and to propose new synonymies. The purpose of this work is also to describe two new species and the previously unknown male of *Aegidinus simulatus* Colby.
Material and methods

The material used in this work is housed in the collections of the following organisations (curators in parentheses):

**BGCO**: Bruce Gill collection, deposited in the Canadian National Collection, Ottawa, Canada (Bruce Gill)

**BMNH**: Natural History Museum, London, United Kingdom (Maxwell Barclay)

**CEMT**: Entomology Sector of the Zoological Collection, Biosciences Institute, Federal University of Mato Grosso, Cuiabá, Brazil (Fernando Vaz-de-Mello)

**CMN**: Canadian Museum of Nature, Ottawa, Canada (François Génier)

**IRSNB**: Belgian Royal Institute of Natural Sciences, Bruxelles, Belgium (Alain Drumont)

**MNHN**: National Museum of Natural History, Paris, France (Olivier Montreuil)

**OUMNH**: Oxford University Museum, Oxford, United Kingdom (Darren Mann)

**RMNHL**: Royal Museum of Natural History Naturalis, Leiden, Netherlands (Hans Huijbregts, Jan Krikken)

**UNMSM**: Natural History Museum, National University Mayor de San Marcos, Lima, Peru (Angélico Asenjo, Luis Figueroa)

**ZIN**: Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia (Andrey Frolov)

Morphological terminology follows Frolov (2012) and Frolov and Akhmetova (2016). Labels of the type specimens are cited verbatim and separated by a slash, and our comments are in square brackets. The holotypes of the new species are supplied with red labels ‘HOLOTYPUS Aegidinus [species name] Frolov, Akhmetova & Vaz-de-Mello 2018’; the paratypes are supplied with yellow labels ‘PARATYPUS Aegidinus [species name] Frolov, Akhmetova & Vaz-de-Mello 2018’. Preparation of specimens, digital images and locality maps follows Frolov et al. (2017a).

Genus *Aegidinus* Arrow, 1904

*Type species*


**Diagnosis**

Body small to mid-sized (length 6 to 12 mm), reddish brown to dark brown. Mandibles subsymmetrical, with long processes on the outer sides. Clypeus with tubercle or horn on anterior margin medially in males, without horn in females. Pronotum variably excavated medially in males, convex to depressed medially in females; anterior margin of pronotum in males with a tubercle or horn medially. Propleura with carinae separating anterolateral areas from basal area. Scutellum narrowly rounded apically, about 1/15 length of elytra. Elytra convex, with marked humeral umbones and striae marked with elongated punctures. Wings fully developed. Metepisternon triangular, its posterior angle rounded to triangular and situated in distinct concavity of epipleuron. Protibiae with three strong outer teeth in both sexes and with a smaller medial tooth in majority of males. Each procoxa with two cavities. Phallobase tube shaped with strongly sclerotised ventral side but without differentiation of ventral and dorsal sclerites. Parameres
relatively short, with complex shape, apices without setae. Gonocoxites separated into two more or less distinct parts.

*Aegidinus* is distinct among the orphnines in having the following unique characters: mandibles with processes on the outer sides; shape of the gonocoxites is diverse and species specific at least in majority of species; procoxae with two cavities each; parameres are asymmetric in two species; phallobase with protruding ventroapical plate in some species. From other Aegidiini, *Aegidinus* also differs in the absence of a hole connecting mesocoxal cavities, and in having more or less distinct transverse carina on metatibiae.

**Diagnostic characters of species**

Most *Aegidinus* species are similar externally and, despite some interspecific variation of the body sculpture and head and protoracic armature in some species, reliable identification is only possible by examining the shape of the male genitalia. External female genitalia (gonocoxites) are also highly specific, although their usefulness in distinguishing closely related species requires further evaluation (see Discussion below).

**Species composition and distribution**

*Aegidinus* comprises 14 species including two newly described in this work. Members of the genus occur in South America, mostly in the Amazon and Guianan moist forest regions to Yungas in the west, and on the island of Trinidad (Figure 7).

**Key to Aegidinus species (males)**

1. Parameres separated into dorsomedical and ventrolateral lobes (Figures 1(h,i), 2(e,f) and 3(b–d))....................................................................................................................................................... 2
   - Parameres not separated into dorsomedical and ventrolateral lobes (Figure 6(c–e))...
     ......................................................................................................................................................... *Aegidinus cornutus*

2. Phallobase with ventroapical plate (Figures 1(g), 3(c) and 4(d))....................................................... 3
   - Phallobase without ventroapical plate (Figures 2(d), 4(h) and 5(d)).............................. 6

3. Parameres symmetrical.......................................................................................................................... 4
   - Parameres asymmetrical.................................................................................................................... 5

4. Ventrolateral lobe of paramere with subapical tooth (Colby 2009, fig. 55)................................. 
   - Ventrolateral lobe of paramere without subapical tooth (Figure 1(h))................................. 
     ......................................................................................................................................................... *Aegidinus howdenorum*

5. Parameres longer, more asymmetrical (Figure 4(b,c)); ventroapical plate of phallobase longer than wide (Figure 4(d)); protibia without medioapical tooth.................................................................. 7
   - Parameres shorter, less asymmetrical (Figure 3(b,d)); ventroapical plate of phallobase wider than long (Figure 3(c)); protibia with medioapical tooth ................................. *Aegidinus candezei*

6. Mediobasal margins of dorsomedical lobes of parameres feebly sclerotised, membranous (Figure 2(e)); protibia with medioapical tooth........................................................................................................ 7
- Mediobasal margins of dorsomedial lobes of parameres strongly sclerotised (4G, 5E); protibia without medioapical tooth ........................................................................................................... 9

7. Ventrolateral lobes of parameres long and slender (in lateral view), noticeably longer than dorsomedial lobes (Figure 2(f))...................................................................................................................... steinheili

Figure 1. Aegidinus guianensis, holotype, female (a, b, d), female, paratype of Ae. oreibates (c), female from Villa Napoleão, Brazil (e), male, holotype of Ae. oreibates (f), male, paratype of Ae. oreibates (g–i). Habitus in dorsal view (a, c, f), labels (b), female external genitalia (d, e), aedeagus in lateral (h) and ventral view (g), parameres in dorsal view (i).
- Ventrolateral lobes of parameres triangular and obtuse in lateral view, not longer than dorsomedial lobes ................................................. 8

8. Ventrolateral lobes of parameres as long as dorsomedial lobes...... *Aegidinus petrovi*
- Ventrolateral lobes of parameres noticeably shorter than dorsomedial lobes.................. ................................................................. *Aegidinus teamscaraborum*

**Figure 2.** *Aegidinus steinheili*, lectotype, male (a, d–f), male with erroneous label ‘Bresil Steinheil.’ (b), female, paralectotype (c, g). Habitus in dorsal view (a–c), female external genitalia (g), aedeagus in lateral (f) and ventral view (d), parameres in dorsal view (e).
9. Dorsal sides of parameres strongly overlapping and separated by slit (Figure 4(f), arrowed).......................................................... ..........................................................

Aegidinus simulatus

Figure 3. Aegidinus spp. Aegidinus candezei, lectotype, male (a, e), male (b–d), female (h, k), female, holotype of Ae. sunidigea (g, j); Aegidinus sp., paralecotype of Ae. candezei (f, i, l). Habitus in dorsal view (a, g, h, i); labels (e, f); female external genitalia (j–l); aedeagus in lateral (b) and ventral view (c); parameres in dorsal view (d).
- Dorsal sides of parameres less overlapping and not separated by slit (Figure 5(f)) 10

10. Dorsal processes of parameres carina shaped (Figure 5(e), arrowed)..........................

................................................................................................................................. Aegidinus colbyae sp. nov.
- Dorsal processes of parameres tooth or spur shaped..................................................... 11

11. Dorsal processes of parameres long, spur shaped............... Aegidinus brasiliensis
- Dorsal processes of parameres short, tooth shaped............... Aegidinus howeae

Figure 4. Aegidinus spp. Ae. noriegai sp. nov., holotype (a–d), Ae. simulatus, male (e–h). Habitus in dorsal view (a, e); aedeagus in lateral (b, f) and ventral view (d, h); parameres in dorsal view (c, g).
Figure 5. *Aegidinus colbyae*, holotype male (a, e, d, f), paratype female (b, c). Habitus in dorsal view (a, b); female external genitalia (c); aedeagus in lateral (f) and ventral view (d); parameres in dorsal view (e).
Aegidinus guianensis (Westwood, 1845)
(Figure 1(a–i))

*Aegidium guianense* Westwood, 1845: 175

= *Aegidinus oreibates* Colby, 2009: 26, syn. nov.

= *Aegidinus crypticus* Colby, 2009: 20, syn. nov.

**Type locality.** Guyana, Upper Takutu-Upper Essequibo.

**Type material examined**

*Aegidium guianense*: holotype (Figure 1(a)), female at OUMNH labelled ‘Guiana/Aegidium ? Guianense Westw./TYPE WESTWOOD Trans. Ent. Soc L.1846.P.175 T. 12. 8. 5. Coll. Hope Oxon./TYPE COL: 488 Aegidium guianensis Westw. HOPE DEPT. OXFORD/W/WB’.


**Additional material examined**

**VENEZUELA. Bolivar:** Guri, dry forest, 14 June 1996, H. Howden and A. Howden leg., one female (CEMT); Guri, wet forest, 17 June 1996, B.D. Gill leg., one female (BGCO).

**TRINIDAD AND TOBAGO.** 11 km SE Arima, Arena Forest Reserve, 80 m, rainforest, FIT, 13–22 June 1993, S. Peck, J. Peck leg., one male (BGCO); 8 km N Arima, Simla Research Station, 260 m, lower montane rainforest FIT, 6–14 June 1993, S. Peck, J. Peck leg., one
male (BGCO); 16 km N Arima, Andrews Trace, 620 m, upper montane rainforest, FIT, 24 June–7 July 1993, S. Peck, J. Peck leg., one male (BGCO); 8 km N Arima, Simla Research Station, 260 m, lower montane rainforest, FIT, 24 June–8 July 1993, S. Peck, J. Peck leg., one female (BGCO). **GUYANA. Potaro-Siparuni:** Pataro-Siparuni Iwokara Rain Forest, 70 m, human faeces baited, 13 April–31 May 2009, S. Phelps leg., one female (OUMNH). **SURINAME.** Road to Amotopo, km 39, unbaited pitfalls, secondary forest, 29 May–2 June 1981, J. Huijbregts leg., one female (RMNHL); Sipaliwini W-bank Suriname River opposite Pingpe 4.041667°N, 55°45W, FIT in forest, 25 January–1 February 2012, M.A. Hielkema leg., one female (RMNHL); road to Amotopo, km 34, primary forest, pitfalls baited with human dung, 28 May–1 June 1981, J. Huijbregts leg., one female (RMNHL). **FRENCH GUIANA.** Mont Grand Matoury, 24 January 2013, SEAG leg., two females (ZIN); 7 January 2013, SEAG leg., one male (ZIN); Gourdonville, 1905, E. Le Moult leg., one male and one female (MNHN). **BRAZIL. Roraima:** Cariri, Vila Napoleão, 4 May 1972, J. Celso leg., one male (CEMT); 10 April 1972, J. Celso leg., one female (CEMT). **Pará:** Belém, one female (MNHN).

**Diagnosis**

_Aegidinus guianensis_ is most similar to _Ae. howdenorum_ but differs from it in having the ventrolateral lobe of the parameres without a subapical tooth (Figure 1(h)). From other _Aegidinus_ species it differs in having the phallobase with a ventroapical plate and symmetrical parameres (Figure 1(g,i)).

**Remarks**

Paulian (1984) and Colby (2009) drew male characters of _Ae. guianensis_ from the type of _Ae. steinheili_, which was considered a synonym of _Ae. guianensis_ after Arrow (1904). Colby (2009) erroneously considered the female specimen with the label ‘Cayenne’, housed in BMNH, to be the holotype of _Ae. guianensis_ and drew the female characters from it. This specimen, in our opinion, belongs to _Ae. howeae_ Colby or _Ae. brasiliensis_, but it lacks the abdomen and genitalia. _Ae. guianensis_ was described from British Guiana (nowadays Guyana) and the holotype of it is housed in OUMNH (Figure 1(a,b)). It agrees with the original description of the species, and its mouthparts were dissected and illustrated by Westwood (1845, pl. XII, fig. 5). The specimen was likely collected by Robert Schomburkg in Pirara on the shores of Lake Amucu (Darren Mann, pers. comm.).

By the shape of the female genitalia and external morphological characters, the type of _Ae. guianensis_ (Figure 1(a,d)) cannot be distinguished from _Ae. oreibates_ Colby (Figure 1(c,e)), described from a long series mostly from the Guiana Shield and the island of Trinidad. For this reason, we propose that _Aegidinus oreibates_ Colby is a synonym of _Aegidium guianense_ Westwood. Because this long series includes both sexes, the male characters of _Ae. guianensis_ can be reliably based on the males from this series.

_Ae. crypticus_ Colby was described from Guyana from a single male specimen. The difference between _Ae. oreibates_ and _Ae. crypticus_ is, according to the author, that in the latter species the median lobes of the parameres are longer and thinner and the shape of the ventral plate of phallobase at the apex is much rounder (Colby 2009). However, the detailed photographs of the parameres provided in the original descriptions (Colby 2009, figs 46–49, 59–60) show that these characters are not diagnostic: the median lobes of the parameres are of about the same length and width and the ventral plates are...
equally rounded. The differences between the photographs are due to the slightly
different angle of view and because the illustrated parameres of Ae. oreibates are
opened while those of Ae. crypticus are close to each other. Therefore, we propose
that Aegidinus crypticus Colby is also a synonym of Aegidium guianense Westwood.

*Aegidinus steinheili* (Harold, 1880), distinct species
(Figure 2(a–g))

*Aegidium steinheili* Harold, 1880: 42
*Aegidinus guianensis* nec Westwood, 1845: 175, auct.: Arrow 1904: 739, 1912: 31; Paulian 1984, 98; Colby 2009: 20

**Type locality.** Colombia, Antioquia, San Carlos.

**Type material examined**

**Lectotype.** Male (Figure 2(a)) at MNHN labelled ‘S. Carlos/Columbia Aegidinus Steinheili Harold/Col. Benderitter ae. guianense/Aegidinus guanensis (Westw.) R. Paulian det./Aegidinus steinheili (Har.) R. Paulian det./Museum Paris/Museum Paris Coll. M. Pic/ HOLOTYPE/Aegidinus guianensis’. The labels of this specimen do not agree completely
with the data provided by Paulian (1984), but we believe that this is the specimen that
Paulian intended to designate as the lectotype. There are cases in which Paulian did not
properly label his material with type labels (Olivier Montreuil, Antoine Mantilleri, pers. comm.). However, this specimen is the only one bearing Paulian’s handwritten identifi-
cation labels and it definitely belongs to the type series from San Carlos.

Additional material examined
COLOMBIA. One male at MNHN, Canoas [not traced locality]. One male at IRSNB labelled ‘Coll. R. I. Sc. N. B. Bresil Steinheil. ex coll. Candèze/Aegidium Alatum Cast. Br./Aegidinus guianensis (Westwood) det. J.B. Colby 2008’; a mislabelled specimen (see below) most probably collected in San Carlos.

Diagnosis
*Aegidinus steinheili* is most similar to *Ae. petrovi* Colby and *Ae. teamscaraborum* Colby but differs from them by having ventrolateral lobes of parameres long and slender (in lateral view), noticeably longer than dorsomedical lobes (Figure 2(d–f)). The female has a punctation of the body similar to that of the male (Figure 2(c)); the external female genitalia are as in Figure 2(g).

Remarks
Arrow (1904) considered *Ae. steinheili* (Harold 1880) to be a synonym of *Ae. guianensis* (Westwood 1845) although he did not study the genitalia of the specimens. Paulian (1984) and Colby (2009) followed Arrow, apparently because they did not study the type of *Ae. guianensis* and thus misinterpreted this species. Examination of the female type of *Ae. guianensis* and conspecific males (see above) showed that *Ae. steinheili* is distinct from it and all other *Aegidinus* species.

Paulian (1984) studied most of the *Aegidinus* specimens from San Carlos and one from Nare and, based on the external characters, identified them as two species, *Ae. steinheili* (= *Ae. guianensis* sensu Paulian) and *Ae. candzei*. He designated the larger male from San Carlos, with the denser punctation of the body, as the lectotype of *Ae. steinheili* (Figure 2(a)). We dissected all specimens of this series and found that characters of the male and female genitalia are congruent with the characters of the external morphology. In this material we found two male morphotypes and two female morphotypes and we agree with Paulian that they belong to the two species mentioned above.

In the collection of IRSNB there is a male specimen of this species with the labels ‘Coll. R.I.Sc.N.B. Bresil Steinheil. ex coll. Candèze/Aegidium Alatum Cast. Br./Aegidinus guianensis (Westwood) det. J.B.Colby 2008’. It was among a small series of *Aegidiellus alatus* Laporte de Castelnau having the same printed labels ‘Coll. R.I.Sc.N.B. Bresil [. . .]’ but with varying additional data. These labels were placed by IRSNB technical staff under previously unlabelled specimens that were in the collection drawer next to the bottom label ‘Aegidiellus alatus’. The record of *Ae. steinheili* from Brazil (Colby 2009, as *Ae. guianensis*) is apparently based on this mislabelled specimen which is very similar to the larger males of the type series (Figure 2(b)).

*Aegidinus candzei* (Preudhomme de Borre, 1886)  
(Figure 3(a–e,g,h,j,k))

*Orphnus candzei* Preudhomme de Borre, 1886: 116  
*Aegidinus candzei* (Preudhomme de Borre); Arrow, 1912: 31; Schmidt, 1913: 76; Paulian 184: 89; Colby 2009: 17  
*Aegidinus sunidigea* Colby, 2009, syn. nov.
**Type locality.** Colombia, Chocó.

**Type material examined**

**Lectotype** (designated here, *Figure 3(a,e)*), male at IRSNB labelled ‘Coll. R. I. Sc. N. B. Colombie ex coll Candeeze Choco Wallis/det. P. de Borre 1886 Orphnus Candeezi ♀Type/ Holotype/Lectotypus Orphnus candeezi P.d.B. Frolov des. 2018’.

**Paralectotype** (*Figure 3(f,i,l)*), female at IRSNB labelled ‘Coll. R. I. Sc. N. B. Colombie: Choco ex Wallis ex coll. Candeeze/det. P. de Borre 1886 Orphnus Candeezi ♀Type/ Allotype/Aegidinus candeezi (Preudhomme de Borre) det. J.B.Colby 2009/ Paralectotypus Orphnus candeezi P.d.B. Frolov des. 2018’.

**Additional material examined**

**COLOMBIA. Boyacá:** Otanche, 5 May 1995, Arriágada leg., five females (CEMT).

**Santander:** Puerto Araújo, Los Manantiales Ranch, May 2000, J. Noriega leg., one male (CEMT); Puerto Araújo, Las Marias, 130 m, May 2000, J. Noriega leg., one female (CEMT).

**Tolima:** Mariquita, Municipal forest, 680 m, April 2000, J. Noriega leg., one male (CEMT).

**Antioquia:** Medellín, forest, pitfall, April 1998, J. Noriega leg., one male (CEMT).

**Diagnosis**

*Ae. candeezi* is most similar to *Ae. noriegai* sp. nov. but can be distinguished from it by the shorter and less asymmetrical parameres, ventroapical plate of the phallobase wider than long (*Figure 3(b–d)*), and protibia with medioapical tooth.

**Remarks**

*Aegidinus candeezi* was described with no explicit information about the number of the examined specimens although it was indicated that both sexes were studied. There are two specimens (*Figure 3(a,j)*) in the IRSNB collection which agree with the original description and might be the only specimens studied by Preudhomme de Borre. These specimens should be considered syntypes since no lectotype had been designated so far. The male specimen bears a red printed label that reads ‘Holotype’ (*Figure 3(e)*) and the female specimen the label ‘Allotype’ (*Figure 3(f)*). These labels were placed by the IRSNB technical staff in 1980–2000 (Alain Drumont, pers. comm.). Paulian (1984) mentioned the ‘holotype’ apparently based on these labels. The identity and conspecificity of the two specimens were not questioned by Paulian (1984) and Colby (2009), and the latter author drew the female characters of *Ae. candeezi* from the female syntype. However, we think that the two syntypes are not conspecific. The body punctuation and the shape of the genitalia of the female syntype (*Figure 3(i,l)*) do not agree with the female specimens from San Carlos (*Figure 3(h,k)*) belonging to the series of both sexes with trustworthy locality data. Only the male syntype bears the original locality label ‘Choco Wallis’. The locality label of the female syntype was added by IRSNB technical staff later and put under an unlabelled specimen. Although it seems probable that both specimens originate from Candeeze’s collection and might have been collected by Wallis, the locality of the female syntype is unclear since Wallis made extensive expeditions throughout South America (Veitch 1906).

*Aegidinus sunidigea* Colby was described from a female (*Figure 3(g,j)*) from San Carlos. As discussed above, the series from San Carlos includes two species represented by both
sexes, so the female characters of Ae. candezei can be inferred from these specimens with sparse punctation, including the type specimen of Ae. sunidigea. To ensure stability of the nomenclature, we here designate the male syntype (Figure 3(a)) as the lectotype of Orphnus candezei and propose that Aegidinus sunidigea is a synonym of Orphnus candezei.

**Aegidinus noriegai** Frolov, Akhmetova and Vaz-de-Mello sp. nov. (Figure 4(a–d))

**Type locality.** Colombia, Antioquia, Medellín.

**Type material examined**

**Holotype.** Male (Figure 4(a)) at CEMT labelled ‘COLOMBIA: Antioquia. Porce. Picardia V-1998. pastizal, pitfall. J. Noriega’.

**Diagnosis**

*Aegidinus noriegai* sp. nov. is most similar to *Ae. candezei* but can be distinguished from it by the longer and more asymmetrical parameres, ventroapical plate of the phallobase longer than wide (Figure 4(b–d)), and the protibia without medioapical tooth.

**Description**

**Male** (Figure 4(a)). Body length 8.5 mm. Colour uniformly blackish brown. Anterior margin of frontoclypeus with a horn rounded apically.

Pronotum with widely rounded lateral margins, narrower than elytra, 1.6 times wider than length. Posterior angles widely rounded. Anterior margin bordered, border interrupted medially, with feeble gibbosity. Base of pronotum not bordered, with a few large rounded punctures laterally and a few small medially. Pronotal disc feebly excavated anteromedially, with two gibbosities in centre. Pronotum punctate with a few large rounded punctures laterally and anteromedially and with minute, feebly visible punctures throughout.

Elytra almost as long as wide, widest medially and rounded apically, with humeral and apical humps. First elytral stria as continuous line, connected basally with undulate line from scutellum to humeral hump. Other striae marked with rows of sparse punctures; punctures somewhat V- and comma-shaped on basal part of elytra, becoming smaller towards apices.

Protibia without medioapical tooth.

Aedeagus relatively short and wide, ratio of phallobase length/paramere width 1.8 (Figure 4(b)). Ventroapical plate of phallobase narrow and long, 1/3 as wide as phallobase and longer than wide (Figure 4(d)). Parameres strongly asymmetrical (Figure 4(c,d)): right paramere with relatively long medial and lateral processes, medial process relatively straight; left paramere with vestigial lateral process; medial process curved outwards, with small tooth near apex.

**Distribution**

The species is known from a single locality in Antioquia, Colombian Andes (Figure 7).
**Etymology**
The new species is named after Jorge Noriega (University of Los Andes, Bogotá, Colombia).

*Aegidinus colbyae* Frolov, Akhmetova and Vaz-de-Mello sp. nov.
(Figure 5(a–f))

**Type locality.** Peru, Loreto, Iquitos, Sachamama.

**Type material examined**
Holotype (Figure 5(a,e,d,f)), male at CEMT labelled ‘PERU: LO: IQUITOS SACHAMAMA 100m 22-III-02 CUROE ROTTEN FISH’.
Paratype (Figure 5(b,c)), female at CEMT labelled ‘PERU: LO: IQUITOS SACHAMAMA 100m 22-III-02 CUROE ROTTEN FISH’.

**Diagnosis**
*Aegidinus colbyae* sp. nov. is most similar to *Ae. brasiliensis* Arrow and *Ae. howeae* Colby but can be distinguished from them by the dorsal processes of the parameres being carina shaped (Figure 5(e), arrowed), while this process is tooth or spur shaped in *Ae. brasiliensis* and *Ae. howeae*.

**Description**
*Male* (Figure 5(a)). Body length 10.8 mm. Colour uniformly blackish brown. Anterior margin of frontoclypeus with a long horn rounded apically.

Pronotum with widely rounded lateral margins, almost as wide as elytra, 1.5 times wider than length. Posterior angles widely rounded. Anterior margin bordered, border narrowly interrupted medially, with transversal, bimodal gibbosity. Base of pronotum not bordered, with a row of rounded punctures. Pronotal disc feebly excavated anteromedially, with two gibbosities in centre. Pronotum punctate with a few large rounded punctures laterally and anteromedially and with minute, feebly visible punctures throughout.

Elytra almost as long as wide, widest medially and tapering apically, with humeral and apical humps. First elytral stria as continuous line, connected basally with undulate line from scutellum to humeral hump. Other striae marked with rows of sparse punctures; punctures V-shaped near base, smaller and irregularly elongate on disc.

Protibia without medioapical tooth.

Aedeagus relatively long and slender, ratio of phallobase length/paramere width 2.8 (Figure 5(f)). Ventralapical plate of phallobase absent (Figure 5(d)). Parameres symmetrical, mediobasal margins of dorsomedial lobes strongly sclerotised (5E), dorsal processes of parameres carina shaped (Figure 5(e), arrowed).

Female paratype (Figure 5(b)) differs from male in having relatively wider elytra, pronotum and head without excavations and armature, and in having a protibial spur. Body length 8.5 mm. External female genitalia as in Figure 5(c).

**Distribution**
The species is known from a single locality in Peru: Loreto, Iquitos, Sachamama (Figure 7).
**Etymology**
The new species is named after Julia Colby (Peggy Notebaert Nature Museum, Chicago, USA).

*Aegidinus cornutus* Colby, 2009
(Figure 6(a–f))

*Aegidinus cornutus* Colby, 2009: 18
= *Aegidinus unicus* Colby, 2009: 37, syn. nov.

**Type locality.** Brazil, Mato Grosso, Sinop.

**Type material examined**


**Additional material examined**

**Diagnosis**
*Aegidinus cornutus* can be easily distinguished by the parameres not separated into dorsomedial and ventrolateral lobes (Figure 6(c–e)). External female genitalia as in Figure 6(f).

**Remarks**
*Aegidinus cornutus* and *Ae. unicus* were both described from Sinop, Mato Grosso, Brazil, from a male and a female, respectively. Additional specimens of both sexes with the same locality labels as the holotype and a rather long series of both sexes from Redenção (Figure 6(a,b)) show that the the two names belong to the same species. Therefore, a new synonymy is here proposed.

The label of the paratype of *Ae. cornutus* is wrong. There is no locality ‘Sinópolis’ in Minas Gerais, and Sinop has been probably misinterpreted as an abbreviation; if in the original data the state was noted as MG or MG, it could be confused with Minas Gerais (instead of Mato Grosso). M. Alvarenga went to Sinop (Mato Grosso), then a just founded town, more than once in the 1970s and he was proud of his extensive collecting done there (personal comments to FZVM on several occasions, 1992–2008).
Figure 6. *Aegidinus cornutus*, male (a, c, d, e), female (b, f). Habitus in dorsal view (a, b); female external genitalia (f); aedeagus in lateral (c) and ventral view (e); parameres in dorsal view (d).

*Aegidinus venezuelensis* Colby, 2009

*Aegidinus venezuelensis* Colby, 2009: 38

Type locality. Venezuela, Distrito Capital, Caracas.
Type material examined

**Holotype.** Female at MNHN labelled ‘Vénézuéla Caracas/EX MUSEO N VAN DE POLL/ MUSÉUM PARIS 1936 COLL. A. BOUCOMONT/Aegidinus brasiliensis R. Paulian det. Arr./ Aegidinus venezuelensis Colby HOLOTYPE’.

Remarks

The type of this species cannot be reliably distinguished from *Ae. guianensis* and *Ae. howdenorum* females. Distribution suggests that it may belong rather to *Ae. howdenorum*, but additional material is needed. It should be noted that *Ae. howdenorum* is known from a pair of specimens; the third female from ‘Colombia’ was tentatively identified as *Ae. howdenorum* and cannot be distinguished from females of *Ae. guianensis*. Considering the similarity of the two species – *guianensis* and *howdenorum* differ only in a slightly different shape of the parameres, the difference smaller than in other Aegidinus species – additional material is also needed to clarify whether this difference is not due to the geographic variability among populations of one species.
**Aegidinus simulatus** Colby, 2009
(Figure 4(e–h))

_Aegidinus simulatus_ Colby, 2009: 32

**Material examined**


**Diagnosis**

*Aegidinus simulatus* is similar to _Ae. brasiliensis_, _Ae. howeae_ and _Ae. colbyae_ sp. nov. in having mediobasal margins of the dorsomedial lobes of the parameres strongly sclerotised, but can be distinguished from them by having the dorsal sides of the parameres strongly overlapping and separated by a slit (Figure 4(f), arrowed).

**Description of male**

Body length 9.5–10.0 mm. Colour uniformly blackish brown. Anterior margin of frontoclypeus with a horn rounded apically (Figure 4(e)).

Pronotum with widely rounded lateral margins, narrower than elytra, 1.6 times wider than length. Posterior angles widely rounded. Anterior margin bordered, border narrowly interrupted medially, with short, somewhat bimodal tubercle. Base of pronotum not bordered, with obsolete punctures laterally. Pronotal disc feebly excavated anteromedially, with two gibbosities in centre. Pronotum punctate with a few large rounded punctures laterally and transversely elongated punctures anteromedially and with minute, feebly visible punctures throughout.

Elytra almost as long as wide, widest medially and rounded apically, with humeral and apical humps. First elytral stria as continuous line not connected basally with undulate line from scutellum to humeral hump. Other striae marked with rows of sparse elongate punctures.

Protibia without medioapical tooth.

Aedeagus relatively long and slender, ratio of phallobase length/paramere width 2.6 (Figure 4(f)). Ventroapical plate of phallobase absent (Figure 4(h)). Parameres symmetrical, mediobasal margins of dorsomedial lobes strongly sclerotised (4G), dorsal sides of the parameres strongly overlapping and separated by a slit (Figure 4(f), arrowed).

**Distribution**

The species was described from Aliñahui (Ecuador, Napo Province) and Gigante (Huila, Colombia). The new records are from Curaray River (Peru, Loreto) and San Martín (Colombia, Meta) (Figure 7).

**Discussion**

**Species descriptions**

Some nominal species of _Aegidinus_ were described from males, other from females, and still others from both sexes (Arrow 1904; Paulian 1984; Colby 2009). However, the
conspicuous of the sexes was not always verified in the last case. We think that the species delimitation and description methodology should be consistent in studies of Orphninae, and thus the species should be described from the males only. Identification of the females should be based at least on a series of both sexes collected together, if the more reliable methods (e.g. in copula collecting) are not possible. We have examined a few series of specimens collected in one locality and thus we were able to assess the conspecificity of the males and females of some species; this is not yet possible for all nominal species, however.

**Taxonomic and diagnostic characters**

_Aegidinus_ is unique among the Orphninae in having a large variation in the shape of the gonocoxites (Colby 2009). However, whereas the usefulness of the male genitalia in the classification of the Scarabaeoidea in general and Orphninae in particular is proved by the majority of the available taxonomic works, utilisation of the female genitalia requires further research. Data about utilisation of the female genitalia in the Scarabaeidae at the species level are scarce. Özgül-Siemund and Ahrens (2015) showed that the female genitalia can provide species-level taxonomic characters in Sericinae, but these characters pertain to the secondary sclerotisations in the internal genitalia (ductus bursae) rather than to the external genitalia. Similar structures are absent in the Orphninae. Detailed examination of the female genitalia of a reasonable number of _Aegidinus_ specimens dissected by a standardised procedure (Frolov et al. 2017a) confirmed species-specific differences in most species but also showed that the differences between similar species are difficult to interpret unequivocally, although these species can be rather reliably distinguished by the shape of the male genitalia. Therefore, we consider the shape of the external female genitalia in _Aegidinus_ to be a species-group or subgenus-level character rather than a species-level character. As in the other Scarabaeoidea, description of the species from females may result in an unstable classification.

One of the supposedly informative _Aegidinus_ female genital structures, vaginal palps (stili), proved non-reliable since they are subject to both intraspecific and interspecific variation. We found _Aegidinus_ specimens of different species having partly segmented coxites as well as those having asymmetrical genitalia with only one coxite having a distinct stylus. Some species include specimens with stili and specimens without. The mechanism of the development of such aberrations is probably the same as that involved in symphysocery: premature termination of the segmentation during ontogenesis. Symphysocery, the incomplete segmentation of the antennomeres, is found in different groups of scarab beetles and is thought to be highly homoplastic (Krell 1992; Ahrens 2006; Frolov and Akhmetova 2016). Stili are known in many higher groups of the Scarabaeoidea (Dupuis 2005) but there is no apparent taxonomic pattern. Stili are also found in the majority of the Orphninae taxa but are subject to reasonable variability, both intraspecific and interspecific (AVF unpublished data). Therefore, we consider segmentation of the coxites (presence or absence of distinct stili) as a character of low phylogenetic, taxonomic and diagnostic value and thus do not use it in taxon delimitation or identification.
Phylogenetic relationships of *Aegidinus*

*Aegidinus* was placed in the tribe *Aegidiini* by Paulian (1984), and this placement was supported by Colby (2009) and Frolov (2012). Paulian (1984) did not discuss the phylogenetic relationships within the *Aegidiini*. Colby (2009) provided strict consensus trees of the two phylogenetic analyses, one of which resulted in the polytomy of the *Orphninae* genera, whereas another suggested the following relationships within the *Aegidiini*: 

\[(Aegidinus + Aegidium) + Aegidiellus + Paraegidium)\]; however bootstrap support for all clades was low. Frolov (2012) suggested that 

\[(Aegidinus + Aegidiellus + Paraegidium)\]

represent a lineage with unresolved relationships, which is sister to *Aegidium*.

Phylogenetic relationships within the *Aegidiini* should be further investigated. Frolov (2012) provisionally placed in this tribe the monotypical genus *Stenosternus* Karsch from São Tomé Island (Guinea Gulf), based on the shape of the metepisternum, a keel separating basal and anterolateral parts of the propleura; the shape of the mandibles; and protibia with a medial tooth. Later examination of the additional material (Frolov and Akhmetova 2015) did not support the placement of *Stenosternus* in the *Aegidiini*. In Frolov’s (2012) analysis, the clade 

\[(Aegidinus + Aegidiellus + Paraegidium)\]

was supported by the single symplesiomorphy, the absence of the protibial process in males. However, in the present work we showed that the process is present in some *Aegidinus* species.

The placement of *Aegidinus* in the *Aegidiini* (excluding *Stenosternus* but including the recently described *Onorius* Frolov and Vaz-de-Mello (2015)) is supported by a few putative synapomorphies: a keel separating basal and anterolateral parts of the propleura (such a keel in *Stenosternus* can be a homoplastic or plesiomorphic state) (Frolov 2012), a tube-shaped phallobase (Frolov 2013), and the stridulatory ridges distinctly curved posteriad (unpublished data of the authors). However, *Aegidinus* differs significantly from the other genera in a number of characters (see Diagnosis for the genus).

Acknowledgements

We are thankful to all curators who provided access to the specimens in their collections. We are especially thankful to Darren Mann (OUMNH) for the information about Robert Schomburgk’s collecting in British Guiana, Oliver Hillert (Schöneiche bei Berlin, Germany) for providing material and help with tracing localities in Venezuela, and Auke Hielkema (Paramaribo, Suriname) and Hans Huijbregts (RMNHL) for help in tracing localities in Suriname. We also thank Daniel Curoe, Jorge Noriega, Celso Godinho, Gerardo Arriágada, Pamela Scheffler and Moacir Alvarenga (in memoriam) for donating specimens used in this study and now belonging to CEMT. Two anonymous reviewers provided comments and corrections that improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Council for Scientific and Technological Development of the Ministry of Science, Technology, and Innovation of Brazil, CNPq [405697/2013-9, 440604/2015-0, 400681/2014-5, 306745/2016-0] and partly by the Russian Foundation for Basic Research [grant...
The study was completed in the framework of the Russian state research project AAAA-A19-119020690101-6.

ORCID
Andrey V. Frolov http://orcid.org/0000-0002-6724-6828
Lilia A. Akhmetova http://orcid.org/0000-0002-2151-1278
Fernando Z. Vaz-de-Mello http://orcid.org/0000-0001-9697-320X

References


Preudhomme de Borre A. 1886. Liste des Lamellicornes Laparostictiques recueillis par feu Camille Van Volxem pendant son voyage au Brésil et a la Plata en 1872, suivie de la description de dix huit espèces nouvelles et un genre nouveau. Annales de la Societe entomologique de Belgique. 30:103–120.


Veitch JH. 1906. Hortus Veitchii: A history of the rise and progress of the nurseries of Messrs. James Veitch and Sons, together with an account of the botanical collectors and hybridists employed by them and a list of the most remarkable of their introductions. London: J. Veitch and Sons; p. 684 p.