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Earthworm species in *Musa* spp. plantations in Brazil and worldwide

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Abstract

Bananas and plantains are major commodity/food crops that represent an important habitat for earthworms, although so far, no review is available on earthworm communities associated with banana/plantain crops worldwide. The Vale do Ribeira region is among the largest banana producing areas in Brazil, but little is known of the earthworms living there. Hence, the present study assessed earthworm populations and species in three banana plantations and adjacent Atlantic forest fragments along the Ribeira de Iguape River using standard (hand sorting) methodologies. Furthermore, we review earthworm populations reported in banana/plantain plantations worldwide. Only two species (*Pontoscolex corethrurus*, *Amynthas gracilis*) belonging to two families (Rhinodrilidae, Megascolecidae) were found in the Ribeira River valley, occurring concurrently. Abundance was low (< 13 indiv. m^{-2}) compared with other banana plantations worldwide, that frequently surpassed 100 indiv. m^{-2}. More than 70 studies reported earthworms from >200 banana plantations in 28 countries, and mean species richness was 2.7 per site, ranging from 1 to 10 species. Exotics predominated in most sites and *P. corethrurus* was the most prevalent species encountered. Overall, more than 104 species from 10 families were reported, with around 61 native and 43 exotic widespread species, mainly of the Megascolecidae, Lumbricidae and Acanthodrilidae families. Richness was highest in India (27 spp.) and the Canary Islands (25 spp.), but native species dominated only in a few countries and sites, while exotics were prevalent especially in island countries and Brazil. Lower-input practices appear to be important for earthworm communities and banana plantations can have large earthworm populations in some cases, which may be contributing to soil processes and plant production, topics that deserve further attention. However, many important banana-producing countries have not yet been evaluated, so further work is warranted, both in terms of applied ecology and biodiversity.

Keywords
Annelida, banana, biodiversity, Oligochaeta, plantain, *Pontoscolex corethrurus*

Introduction

Bananas and plantains are large, perennial herbs belonging to the genus *Musa*, that evolved in Indochina and Southeast Asia, but with major secondary diversification in Africa, India and the Caribbean (Price 1995). Bananas are a major commodity, occupying over 6 million ha (FAO 2018) and representing an important contribution to the economy of many developing countries worldwide (OECD/FAO 2019). Plantains resemble bananas, but are generally longer, have more starch and are mostly eaten cooked, rather than raw (like the bananas). They are a major staple crop in several African, Asian, Pacific, Latin American and Caribbean countries (Price 1995; Norgrove and Hauser 2014). In 2018, the six main banana producers (total production) were India, China, Indonesia, Brazil, Ecuador and the Philippines, while the six countries with the greatest surface area devoted to banana production were India (884,000 ha), Tanzania (490,701 ha), Philippines (484,247 ha), Rwanda (464,321 ha), Brazil (449,284 ha) and China (383,216 ha) (FAO 2018). India accounts for around 24% of global production and Brazil around 5% (FAO 2018), while the whole of Latin America and the Caribbean (LAC) region account for around 25% of the world's banana production (OECD/FAO 2019).

Throughout much of LAC, bananas and plantains are still cultivated at the subsistence level, often in agroforestry systems (Harvey and Villalobos 2007; Malézieux et al. 2009; Paul et al. 2015; Coelho 2017; Garcia et al. 2017; Salazar-Díaz and Tixier 2017). However, commercial plantations are also widespread, occupying large monoculture areas, particularly in warmer, wetter regions of the tropics (Campbell 2018; Yahia 2019). In Brazil, most of the area devoted to banana cultivation lies within the Atlantic Rainforest biome, a highly threatened hotspot of biodiversity (Myers et al. 2000). In fact, much of the banana and plantain cultivation worldwide is performed in wetter tropical climates, and frequently close to rainforest ecosystems, where they may represent a potential hazard to biodiversity conservation. In commercial plantations, conventional production practices are adopted, including frequent herbicide use to control weeds, fumigation to control fungal diseases (particularly *Fusarium* and *Pythium*) and root nematode infestation, as well as Sigatoka (Marin et al. 2003; Cordeiro et al. 2004; Gasparotto et al. 2006), although some resistant varieties for the latter are already available (Timm et al. 2016; Dale et al. 2017). These practices may have important negative impacts on earthworm populations (da Silva et al. 2006; Baretta et al. 2011), despite the high amounts of litter inputs, which represent C (food) sources for soil biota, and protection from soil erosion (Lombardi Neto and Moldenhauer 1992). Worldwide, however, little is known of the soil biota inhabiting banana plantations, and so far, there has not been an overview of true soil-inhabiting animals in banana plantations worldwide.

Earthworms are essential service providers for terrestrial ecosystems (Lavelle et al. 2006). Their activity, generating galleries and casts, contributes to formation and maintenance of soil structure (Lavelle 1997; Capowiez et al. 2012), increasing porosity, infiltration and water retention (Fiuza et al. 2012), as well as re-distribution and breakdown of soil organic matter (Brown et al. 2000). However, earthworms are sensitive to land use and management, and can be used as soil quality and management as well as environmental bioindicators (Brown and Domínguez 2010; Bartz et al. 2013; Bünemann et al. 2018). Brazil is home to more than 300 described earthworm species (Brown et al. 2013), but practically nothing is known of the species and populations inhabiting banana plantations in the country.

The Vale do Ribeira region, located in northeastern Paraná State and southern São Paulo State, has extensive areas (over 36,000 hectares; ABAVAR 2015) devoted to banana cultivation (Bueno 2003). In this region, banana fields are normally surrounded by Atlantic forest fragments (Cordeiro et al. 2017), that have been reduced to around 12% of their original surface area (Ribeiro et al. 2009). Although frequently disturbed with various management practices, banana plantations are perennial crops that could provide adequate habitats for the establishment of native earthworm species, especially when Atlantic forest fragments occur surrounding banana cropping areas (Cordeiro et al. 2017). However, little is known about the effects of banana crops on abundance and diversity of earthworm species, and the occurrence of these invertebrates in Atlantic forest fragments in the Ribeira valley region. Furthermore, little is known of the presence of native and exotic earthworm species in banana and plantain fields worldwide. Hence, the present study was undertaken to assess earthworm populations in banana plantations and native forest fragments in the Ribeira de Iguape River valley in the State of São Paulo, and evaluate earthworm communities (abundance, biomass, species composition) associated with banana and plantain crops worldwide.

Material and methods

Study sites in the Ribeira de Iguape River valley

Three counties in the lower Ribeira River valley, all of them in the State of São Paulo were selected for this study: Eldorado, Sete Barras and Registro (Fig. 1). The climate in Sete Barras and Registro is rainy tropical (Af-type according to Köppen), with mean rainfall greater than 60 mm in the driest month. In Eldorado, climate is Köppen Am tropical, with rainfall less than 60 mm in the driest month. The average annual rainfall for all counties ranges from 1500 to 1600 mm (CEPAGRI 2018; CIIAGRO 2018), with the highest concentration of rains occurring from January to March. The mean

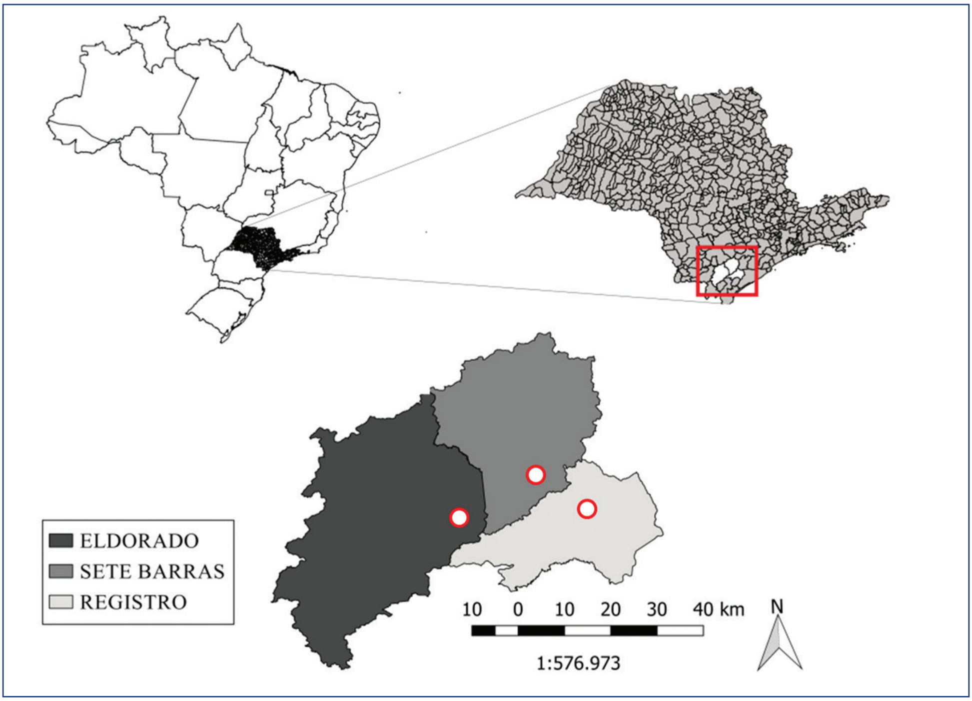

Figure 1. Location of the counties sampled in the Ribeira de Iguape River valley, São Paulo State, Brazil.

Table 1. Land use system, watershed number (WN), age of the land use, geographic coordinates and soil types according to FAO classification (IUSS/WRB 2015) of the sites evaluated in each county of the Ribeira de Iguape River Valley, São Paulo, Brazil.

Site	County	System	WN[1]	Age (yrs)	Latitude, Longitude	Soil types
1	Eldorado	Banana	344	50	24°29'35"S, 48°02'10"W	Cambisols
2	Eldorado	Atlantic forest	344	> 50	24°30'09"S, 48°02'30"W	Cambisols
3	Sete Barras	Banana	422	15	24°23'34"S, 47°53'51"W	Cambisols
4	Sete Barras	Atlantic forest	422	> 50	24°23'30"S, 47°53'22"W	Cambisols
5	Registro	Banana	379	40	24°26'56"S, 47°49'41"W	Cambisols / Histosols
6	Registro	Atlantic forest	389	45	24°26'47"S, 47°49'23"W	Cambisols / Histosols

[1] Official cartographic number for the watershed.

annual temperature ranges from 23.9 to 24.3 °C, with the lowest temperature (13 °C) in July and highest (34.2 °C) in February. Soils in the valley originate from sedimentary, metabasic and amphibolic rocks (Oliveira et al. 2002), with high natural fertility (calcium, magnesium, potassium, and phosphorus content) and high organic matter levels, due to seasonal river floods that deposit alluvial material. Soil texture varies from loam to clay. The areas chosen in the three counties are characterized by smaller watersheds that flow into the Ribeira River with banana crops on the high ground level and Atlantic forest sites (control sites) in advanced stages of regeneration close to the Ribeira River. General characteristics of the areas are given in Table 1.

Earthworm sampling

Earthworms were collected using an adaptation of the standard sampling method proposed by the Tropical Soil Biology and Fertility (TSBF) Programme (Anderson and Ingram 1993). In each area 10 samples (25 × 25 cm square to 20 cm depth) were taken, divided into 2 equally-numbered transects with samples every 20 m. Distance between transects was ca 10 m. Earthworms were hand-sorted from the soil in the field and fixed in 80% alcohol. In the laboratory, earthworms were identified to species or family level (juveniles) using taxonomic keys (Michaelsen 1900; Righi 1990; Blakemore 2002). The material was deposited in the Fritz Müller Oligochaete collection (COFM) at Embrapa Forestry in Colombo, Brazil. The earthworm data obtained were used to determine the total species abundances (no. individuals and fresh mass m^{-2}) and richness, per site and land use (banana, forest).

Literature review

Both the common and scientific names of banana were used for a bibliographic search online using the keywords for bananas and plantains in English, Portuguese, French and Spanish: *Musa* (genus), *Musa acuminata*, *Musa balbisiana*, banana, banane, banano, plátano and plantain. These were then crossed with the common names of earthworms in these languages: earthworms, minhoca, oligochaeta, oligoqueta, vers de terre and lombriz de tierra. Online scientific databases Web of Science, Science Direct, Scielo, google academic and the Base de Dados de Teses e Dissertações (BDTD – Thesis and Dissertation Database) of Brazil were consulted. All the resulting publications were consulted and those containing data on earthworm abundance (density and/or biomass) or species identification were selected and these data extracted, as well as information on sampling sites (counties, countries, management practices of the plantations). Earthworm species were separated into different families and into native or exotic to the region of occurrence, and species richness per site and for each group (native, exotic), when available. Although we treated bananas and plantains separately when possible, for most of the analysis we considered them together, since not all publications provided details regarding the types of bananas cultivated, and even plantains are often called 'bananas.' Details on the species and management data obtained and presented in this paper are available for download online from the open access repository Mendeley Data at http://dx.doi.org/10.17632/p8ywsnj8c5.1 (Cremonesi et al. 2020).

Data treatment

Quantitative data on the earthworm abundance and biomass obtained from the literature and from the present study were treated as follows. Means of earthworm abundance (no. individuals m^{-2}) and biomass (fresh mass in gm^{-2}) were calculated per sampling site (plantation), using data from the present study. When quantitative data from the literature was available for the individual site, it was used as is. When only means for several plantations in the same general location were provided, these were also used. As the interest of the present study was more at the spatial (site-level) rather than the temporal scale, when samples were taken on multiple occasions, and individual means per sampling date were not available, overall means were used. When taken in wet and dry seasons, both values were used as an interval of abundance and biomass (when measured).

Results and discussion

Specimens examined from the Ribeira de Iguape River valley sites

Family Rhinodrilidae

Pontoscolex (Pontoscolex) corethrurus (Müller, 1857)

COFMBRSP0231, 1 individual in Atlantic Forest, HMN 389, Registro – SP (24°26'16.85"S, 47°49'31.71"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0232, 2 individuals in Atlantic Forest, HMN 389, Registro – SP (24°26'16.82"S, 47°49'31.71"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0233, 2 individuals in Atlantic Forest, HMN 389, Registro – SP (24°26'16.28"S, 47°49'32.52"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0235, 2 individuals in Atlantic Forest, HMN 389, Registro – SP (24°26'15.71"S, 47°49'33.32"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0236, 1 individual in Atlantic Forest, HMN 389, Registro – SP (24°26'14.57"S, 47°49'35.35"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0238, 2 individuals in banana field, HMN 379, Registro – SP (24°26'54.25"S, 47°49'38.12"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0239, 1 individual in banana field, HMN 379, Registro – SP (24°26'54.81"S, 47°49'39.41"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0240, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.43"S, 47°55'11.56"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0241, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.46"S, 47°55'11.49"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0242, 2 individuals in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'43.79"S, 47°55'24.53"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0244, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'43.93"S, 47°55'10.17"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0245, 3 individuals in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.33"S, 47°55'09.65"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0248, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.90"S, 47°55'08.92"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0249, 1 individual in banana field, HMN 422, Sete Barras – SP (24°23'38.61"S, 47°55'23.49"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0251, 1 individual in banana field, HMN 422, Sete Barras – SP (24°23'43.01"S, 47°55'24.52"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0252, 3 individuals in banana field, HMN 422, Sete Barras – SP

(24°23'42.54"S, 47°55'25.32"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0253, 1 individual in Atlantic Forest, HMN 344, Eldorado – SP (24°29'57.34"S, 48°02'41.68"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0255, 1 individual in Atlantic Forest, HMN 344, Eldorado – SP (24°29'55.69"S, 48°02'42.15"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0256, 2 individuals in banana field, HMN 344, Eldorado – SP (24°29'36.89"S, 48°02'09.43"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0258, 2 individuals in banana field, HMN 344, Eldorado – SP (24°29'37.11"S, 48°02'10.84"W), 2019, M. Cremonesi, A. Santos colls.

Rhinodrilidae juveniles. COFMBRSP0246, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.33"S, 47°55'09.65"W), 2019, M. Cremonesi, A. Santos colls.

Family Megascolecidae

Amynthas gracilis (Kinberg, 1867)

COFMBRSP0237, 1 individual in banana field, HMN 379, Registro – SP (24°26'54.25"S, 47°49'38.22"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0250, 3 individuals in banana field, HMN 422, Sete Barras – SP (24°23'38.61"S, 47°55'23.49"W), 2019, M. Cremonesi, A. Santos colls.

Megascolecidae juveniles. COFMBRSP0234, 1 individual in Atlantic Forest, HMN 389, Registro – SP (24°26'16.28"S, 47°49'32.52"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0243, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.06"S, 47°55'10.35"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0247, 1 individual in Atlantic Forest, HMN 422, Sete Barras – SP (24°23'44.33"S, 47°55'09.65"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0254, 1 individual in Atlantic Forest, HMN 344, Eldorado – SP (24°29'56.60"S, 48°02'42.23"W), 2019, M. Cremonesi, A. Santos colls. COFMBRSP0257, 1 individual in banana field, HMN 344, Eldorado – SP (24°29'36.89"S, 48°02'09.43"W), 2019, M. Cremonesi, A. Santos colls.

Earthworm populations in the Ribeira River valley and other sites in Brazil

Only two earthworm species belonging to two families (Rhinodrilidae, Megascolecidae) were found at the six sampling sites in the three counties (Table 2): *Pontoscolex* (*Pontoscolex*) *corethrurus* and *Amynthas gracilis*, both considered peregrine/exotic in southern Brazil (Brown et al. 2006). *Pontoscolex corethrurus* may have originated in the Guyana shield area (Righi 1984), and *A. gracilis* may be native to China (Blakemore 2002). The former species was found living in all sites, while the latter was found in both banana plantations and native forest in Sete Barras and in banana plantations in Registro. At the other sites, only juveniles of the Megascolecidae family were found. These were most likely *A. gracilis* as well, but could not be identified to species level. Maximum richness found per site was similar in banana crops and Atlantic forest fragments (two spp. in each land use), but with some variation between sites (Table 2).

Table 2. Earthworm families, species, and richness in banana plantations and Atlantic Forest remnants, in three counties of the Ribeira de Iguape River valley (Eldorado, Sete Barras, Registro). + means presence and – means absence.

Earthworm family and species	Eldorado		Sete Barras		Registro	
	Banana	Atlantic Forest	Banana	Atlantic Forest	Banana	Atlantic Forest
Megascolecidae						
Amynthas gracilis	–	–	+	+	+	–
Megascolecidae juveniles	+	+	–	+	–	+
Rhinodrilidae						
Pontoscolex corethrurus	+	+	+	+	+	+
Rhinodrilidae juveniles	–	–	–	+	–	–
Species Richness	2	2	2	≥2	2	2

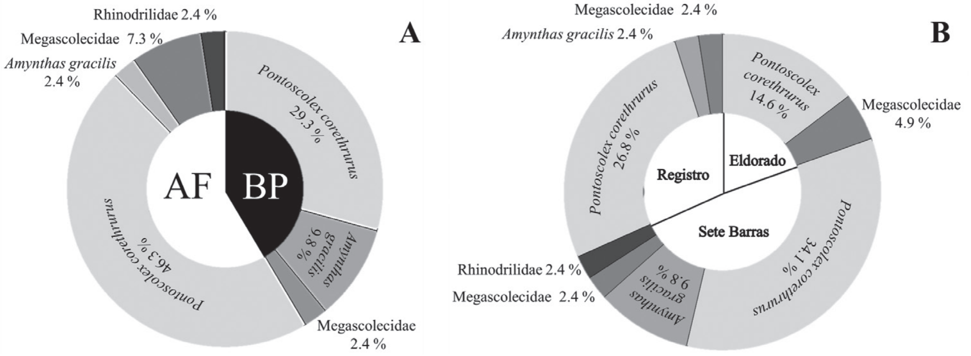

Figure 2. Frequency of earthworm species (% of total individuals collected) in each ecosystem sampled (**A**) in Atlantic Forest (AF) and banana plantations (BP) and by counties (**B**).

Most of the individuals collected (76% of the total) were of *P. corethrurus*, representing 29% of the total abundance in banana crop sites and 46% in Atlantic forest fragments (Fig. 2). *Amynthas gracilis*, although not occurring in all areas, accounted for 12% of all individuals sampled, of which 10% were found in banana crops but only 2% in Atlantic forests. Rhinodrilidae juveniles represented only 2% of the earthworms found, and occurred only in the Atlantic forest, while Megascolecidae juveniles represented 10% of all earthworms, and were often found in Atlantic forest fragments. Both species are widespread in Brazil (Brown et al. 2006), especially in agricultural and disturbed ecosystems, and display relatively high tolerance to a range of abiotic/biotic conditions, which have allowed these species to spread throughout most of the tropics and subtropics worldwide (Brown et al. 2006; González et al. 2006; Taheri et al. 2018). They have also been recommended as indicators of soil quality in agroecosystems and of disturbance in natural landscapes (Nunes et al. 2007; Fernandes et al. 2010).

The predominance of *P. corethrurus* in both native forest and banana plantations of the Ribeira River valley indicate that non-native species have extensively colonized disturbed soils of this region. Nonetheless, this potentially widespread occurrence of exotics should be further evaluated both regionally and nationally, in order to better determine the extent of this phenomenon as well as its possible causes.

Mean overall abundance and biomass of earthworms found in the three sites studied here (6 to 13 indiv. m^{-2} and 2.5 to 9 g m^{-2}) tended to be quite low compared with others observed overall in Brazil (21 to 459 indiv. m^{-2} and 3.1 to 177.4 g m^{-2}; see Table 3). At sites near the Ribeira River valley in the neighboring state of Paraná (Römbke et al. 2009; Maschio et al. 2010), and within the Ribeira River watershed in the nearby Turvo River valley (a tributary of the Ribeira River; Brown et al. 2009), both abundance and biomass were generally much higher (Table 3), even though the predominant earthworm species was the same (*P. corethrurus*). This is probably due to the less intensive and more traditional agroforestry management practices used in these sites, including slashing and mulching, as well as the presence of other trees, particularly atmospheric N_2-fixing leguminous trees, and the absence of or lower pesticide use (Brown et al. 2009; Römbke et al. 2009). These practices may benefit earthworm populations, particularly *P. corethrurus*, as observed comparing a mulched and non-mulched plantation in Antonina, where earthworm abundance was ~13 times higher with mulching (Maschio et al. 2010). Reasons for the lower values found in the Ribeira River valley sites may be due to the more intensive management practices typical of commercial banana plantations in the region, including insecticide and nematicide applications, which may reduce earthworm populations (Clermont-Dauphin et al. 2004).

Earthworm communities in banana plantations worldwide

More than 70 studies were found from 28 countries with data on earthworms in banana and plantain fields (Tables 3, 4, 5). Of these studies, 49 had species data (Table 4; see also full dataset in Cremonesi et al. 2020), coming from ≥ 210 sites (Table 5), of which most were in the Spanish Canary Islands (*N* = 77), mainly due to the intensive sampling efforts of Talavera in Tenerife (Talavera 1992a). Interestingly, two of the major banana-producing countries in terms of area were not represented (Tanzania, Rwanda), and in China (another important producer), only one study reported earthworms from a single site (Sun et al. 2012). Plantain banana fields were sampled in only 22 locations (10% of total) in four countries (Colombia, Cameroon, Ivory Coast and Ecuador; Tondoh 2007; Norgrove et al. 2011; Avilés 2017; Feijoo et al. 2018), and involved traditional management practices, rather than conventional cultivation. Most of the fields evaluated were banana plantations, and only in Ecuador were mixed banana/plantain fields evaluated (Avilés 2017).

Overall, ≥104 earthworm species from 10 earthworm families were recorded from banana/plantain fields worldwide, of which around 61 (59%) were native and 43 exotic to the sampling sites (Table 5). Estimating these numbers is difficult due to insufficient taxonomic resolution in some samples, as well as the uncertain origin of some widespread anthropochores (peregrines transported by humans), particularly in the Megascolecidae family (Blakemore 2002). Highest species richness (27) was observed overall in India, where most of the species found were native (74%). High proportions of native species were also observed in Ivory Coast, Madagascar, and Uganda (possibly 100%) as well as Cameroon (75%), but were lower in Mexico (58%) and Colombia

Table 3. Earthworm abundance and biomass found in banana plantations worldwide, and the predominant species encountered (when available).

Country	Location	Abundance (indiv. m^{-2})	Biomass (g m^{-2})	Predominant species	References
Brazil	Antonina (Monoculture)	71	35.1	*P. corethrurus*	Römbke et al. (2009)
		221	95.7	*P. corethrurus*	
		86	23.8	*P. corethrurus*	
	Antonina (Agroforestry)	173	77.1	*P. corethrurus*	
		338	69.6	*P. corethrurus*	
		117	43.5	*P. corethrurus*	
		21[a]	3.1[b]	*P. corethrurus*	Maschio et al. (2010)
		293[a]	34.9[b]	*P. corethrurus*	
	Adrianópolis (Agroforestry)	211–413[c]	37–71.2[c]	*P. corethrurus*	Brown et al. (2009)
	Barra do Turvo (Agroforestry)	99–176[c]	11.2–17.3[c]	*P. corethrurus*	
		229–459[c]	48.3–117.4[c]	*P. corethrurus*	
	Casimiro de Abreu	~205–440[c]	–	NA	Quintero (2010)
	Paraty	167	–	NA	Correia et al. (2001)
	Eldorado	8	3.9	*P. corethrurus*	This study
	Sete Barras	13	9.0	*P. corethrurus*	
	Registro	6	2.5	*P. corethrurus*	
Cameroon	Mbalmayo Forest Reserve	70	–	*Legonodrilus* sp. nov. 1, *Eminoscolex lamani*	Norgrove et al. (2011)
		121	–	*Legonodrilus* sp. nov. 1, *Eminoscolex lamani*	
	Campo Ma'an	16–92[d]	–	NA	Kanmegne (2004)
Colombia	Quindío (Armenia)	9–16[e]	1.2–3.0[e]	NA[f]	Molina and Feijoo (2016)
Costa Rica	Limón Province (Finca San Pablo)	83–812[g]	–	NA	Agüero et al. (2002)
	Pueblo Nuevo de Villa Franca de Guácimo, Limón	29	6.2	NA	Cornwell (2014)
	Cahuita	350	144.6	*P. corethrurus*	Lapied and Lavelle (2003)
Guadeloupe (France)	Basse-Terre Andosols (mean of 23 sites)	88	23	NA	Clermont-Dauphin et al. (2004)
	Basse Terre Nitisols (mean of 11 sites)	54	17.5	NA	
	Capesterre-Belle-Eau (Gloria Bas)	168	27.6	*P. corethrurus*	Burac et al. (2018)
	Capesterre-Belle-Eau (Source)	288	42.2	*P. corethrurus*	
	Capesterre-Belle-Eau (Bergerie)	188	33.6	*P. corethrurus*	
	Baillif (Sextius)	336	112	*P. corethrurus*	
	Baillif (Grand Canon)	192	70.8	*P. corethrurus*	
	Saint-Claude (Saut d'Eau)	364	46	*P. corethrurus*	
Ecuador	Latacunga (La Maná)	168	–	NA	Avilés (2017)
		111	–	NA	
	Manabí (El Carmen)	78	–	NA	
		37	–	NA	
	El Carmen (Cijádi)	0–145[h]	–	NA	Figueroa (2019)
	El Carmen (Nápoles)	34–144[h]	–	NA	
	Santo Domingo de los Tsáchilas (Santa Patrícia)	83–548[h]	–	NA	
	Santo Domingo de los Tsáchilas (La Floresta)	22–150[h]	–	NA	
India	West Tripura	16–656[i]	4.8–453.6[i]	*P. corethrurus*	Dhar and Chaudhuri (2018)
	Rajapalayam	116	48.8	*Lampito mauritii*, *Perionyx excavatus*	Mariappan et al. (2013)
Ivory Coast	Taabo (Lamto reservation)	186	8.5	*Reginaldia anomala*	Tondoh (1994, 2007)
Martinique (France)	Le Lorrain (Feugère)	244	67.6	*P. corethrurus*	Burac et al. (2018)
	Le Lorrain (Bellevue)	152	43.6	*P. corethrurus*	
	Le Lorrain (Limite)	52	26	*P. corethrurus*	
	L'Ajoupa-Bouillon (Allée Domergue 3)	148	49.6	*P. corethrurus*	
	Basse-Pointe (Fromager Rivière)	80	26	*P. corethrurus*	
	Basse-Pointe (Dantu Bas)	40	9	*P. corethrurus*	

Country	Location	Abundance (indiv. m^{-2})	Biomass (g m^{-2})	Predominant species	References
Mexico	Tabasco, Pablo L. Sidar	25	10	*P. corethrurus*, *Lavellodrilus bonampakensis*	Huerta et al. (2005)
	Tabasco, Teapa	116	20.8	*P. corethrurus*, *Drawida barwelli*, *Polypheretima elongata*	Geissen et al. (2009)
		117	11.8	*Balanteodrilus pearsei*, *Drawida barwelli*	
		94	40.4	*Balanteodrilus pearsei*, *Polypheretima elongata*	
		125	35.6	*P. corethrurus*, *Drawida barwelli*	
		25	8.8	*P. corethrurus*, *Lavellodrilus bonampakensis*	Huerta et al. (2007)
		~350	2.5	*Diplotrema murchiei*	Huerta et al. (2013)
		~350	9.3	*P. corethrurus*	
		~470	16.2	*P. corethrurus*	
		~100	11	*P. corethrurus*	
		~80	2.8	*P. corethrurus*	
		~125	0.8	*Dichogaster* sp.	
Nicaragua	León (Finca Cony)	150	–	NA	Hernández et al. (2015)
	León (Finca San Martín)	325	–	NA	
	León (Finca Santa Isabel)	50	–	NA	
	León (Finca El verdon)	65	–	NA	
	Possoltega (Finca San Joaquin)	150	–	NA	
	Possoltega (Finca Los Ángeles)	225	–	NA	
	Possoltega (Finca Maria de los Ángeles)	100	–	NA	
	Possoltega (Finca Montes Verdes)	125	–	NA	
Philippines	Davao (Sumitomo Fruits Corporation)	~85–175^{j}	–	NA	Fusilero et al. (2013)
		~75–215^{j}		*Metaphire cai*	
South Africa	Kwazulu-Natal (Eshowe)	1500^{k}	180	*Amynthas rodericensis*, *Amynthas minimus*, *P. corethrurus*	Dlamini and Haynes (2004)
Uganda	Kabanyolo University Farm	18–207^{l}	0.1–9.4^{l}	*Dichogaster* sp. 2, *Gordiodrilus* sp. 1	Block and Banage (1968)
	Mabira Forest reserve (1 yr old)	13	0.4	NA	Okwakol (1994)
	(2 yr old)	125	2.2	NA	
	(3 yr old)	131	1.3	NA	
	(5 yr old)	54	0.5	NA	
	(20 yr old)	154	4.2	NA	

[a]Earthworm abundance values were corrected from Maschio et al. (2010) that reported earthworm numbers per sample and not per m^2. [b]Biomass values in g m^{-2} are now included for this study. [c]Mean of dry and wet season samplings, respectively. [d]Mean abundance from eight sites, with four sampled in one year and the other four the subsequent year. [e]Range of abundance taken from eight replicate farms under four different management practices (totaling 32 plantations) in the Armenia region. [f]The identification of the earthworm species collected overall in this study (not by plantation type) is published in Feijoo et al. (2018). [g]Range of abundance found under six weed control treatments (performed on same banana plantation) on five sampling dates; [h]Range of abundance found on six sampling dates in same plantation. [i]Range of abundance and biomass found in three banana plantations. [j]Range of abundance and biomass found on sixteen sampling dates in same plantation. [k]Mean of six banana plantations. [l]Range of abundance and biomass found on eight sampling dates in same plantation.

(53%). In these countries, many of the plantations were managed more traditionally, or using agroforestry, although the low number of sampling sites may also be responsible for these high values, particularly in the former countries. In fact, agroforestry systems had a total of 22 species from nine sites, while conventional production systems had only nine species from 13 sites. Nonetheless, because not enough information was provided in the publications on management practices (not reported in ≥150 sites;

Table 4. Earthworm species, richness and number of native and exotic species found in banana plantations under various management practices worldwide.

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Bangladesh	Lalmonirhat District	NA	NA	*Lampito mauritii*, *Metaphire posthuma*, *Pontoscolex corethrurus*	3	2/1	Reynolds et al. (1995)
Bermuda	Paget Parish	NA	NA	*Amynthas rodericensis*	1	0/1	Reynolds and Fragoso (2004)
	Southampton Parish	NA	NA	*Amynthas hupeiensis*	1	0/1	Reynolds and Fragoso (2004)
Brazil	Antonina, PR	Agroforestry	Monoculture	*Amynthas corticis*, *Pontoscolex corethrurus*, two other spp.	4	0/4	Römbke et al. (2009)
	Antonina, PR	Agroforestry	Monoculture	*Amynthas gracilis*, *Pontoscolex corethrurus*, two other spp.	4	0/4	Römbke et al. (2009)
	Antonina, PR	Agroforestry	Monoculture	*Dichogaster* spp., *Pontoscolex corethrurus*	4	0/4	Römbke et al. (2009)
	Antonina, PR	Agroforestry	Monoculture	*Ocnerodrilus occidentalis*, *Pontoscolex corethrurus*, two other spp.	4	0/4	Römbke et al. (2009)
	Antonina, PR	Agroforestry	Monoculture	*Pontoscolex corethrurus*, one other sp.	2	0/2	Römbke et al. (2009)
	Antonina, PR	NA	Polyculture	*Pontoscolex corethrurus*, one other sp.	2	0/2	Römbke et al. (2009)
	Antonina, PR	Agroforestry	Polyculture	*Dichogaster* sp., *Pontoscolex corethrurus*, and one unidentified sp.	3	?/2	Maschio et al. (2010)
	Antonina, PR	Agroforestry	Polyculture	*Pontoscolex corethrurus*	1	0/1	Maschio et al. (2010)
	Adrianópolis, PR	Agroforestry	Polyculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	Brown et al. (2009)
	Barra do Turvo, SP	Agroforestry	Polyculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	Brown et al. (2009)
	Barra do Turvo, SP	Agroforestry	Polyculture	*Amynthas gracilis*, *Dichogaster* sp., *Pontoscolex corethrurus*	3	0/3	Brown et al. (2009)
	Areia, PB	NA	Polyculture	*Amynthas gracilis*, *Dichogaster affinis*, *Eudrilus eugeniae*, *Pontoscolex corethrurus*	4	0/4	Guerra and Silva (1994)
	Eldorado, SP	Conventional	Monoculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	This study
	Jutaí River margin, AM	NA	NA	*Pontoscolex corethrurus*	ND	0/1	Righi (1990)
	Registro, SP	Conventional	Monoculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	This study
	Sete Barras, SP	Conventional	Monoculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	This study
Cameroon	Mbalmayo Forest Reserve (low density cover)	Organic Agroforestry	Monoculture	*Dichogaster hauseri*, *Eminoscolex lamani*, *Eudrilidae* gen. et sp. nov.1 & 2, *Legonodrilus* sp. nov.1, *Malodrilus kamerunensis*, *Nematogenia panamaensis*, *Rosadrilus camerunensis*	8	7/1	Norgrove et al. (2011)
	Mbalmayo Forest Reserve (high density cover)	Organic Agroforestry	Monoculture	*Dichogaster annae*, *Dichogaster bolaui*, *Dichogaster* sp., *Eminoscolex lamani*, *Eudrilidae* sp., *Eudrilidae* gen. et sp. nov. 1, *Legonodrilus* sp. nov. 1, *Nematogenia panamaensis*, *Ocnerodrilidae* gen. et sp. nov., *Rosadrilus camerunensis*, *Scolecillus tantillus*	10	7/3	Norgrove et al. (2011)
China	Hainan Province	NA	NA	*Pheretima montana*	ND	0/1	Sun et al. (2012)
Colombia	Quindío, Circasia, Barcelona (La Sofe farm)	NA	Monoculture	*Aptodrilus fuhrmanni*, *Amynthas minimus*, *Glossodrilus chaguala*, *Glossodrilus panikita*, *Martiodrilus quimbayaensis*	5	4/1	Feijoo et al. (2018)
	Quindío, Circasia, Barcelona (La Sofe farm)	NA	Polyculture	*Aptodrilus fuhrmanni*, *Amynthas minimus*, *Glossodrilus chaguala*, *Glossodrilus panikita*, *Martiodrilus quimbayaensis*	5	4/1	Feijoo et al. (2018)
	Quindío, Circasia, Barcelona (La Sofe farm)	NA	NA	*Amynthas gracilis*, *Periscolex columbianus*	2	1/1	Feijoo et al. (2018)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Colombia	Armenia, Niagara (La Catalina)	NA	NA	*Amynthas gracilis*, *Glossodrilus griseus*, *Pontoscolex corethrurus*	3	1/2	Feijoo et al. (2018)
	Quindio, Calarcá, Quebrada Negra	NA	NA	*Glossodrilus griseus*	1	1/0	Feijoo et al. (2018)
	Quindío, Marmato (La Cristalina farm)	NA	Monoculture	*Glossodrilus lacteus*	1	1/0	Feijoo et al. (2018)
	Quindío, Marmato (La Cristalina farm)	NA	Polyculture	*Glossodrilus lacteus*	1	1/0	Feijoo et al. (2018)
	Quindío, Marmato (La Cristalina farm)	NA	NA	*Dichogaster affinis*	1	0/1	Feijoo et al. (2018)
	Armenia, La Revancha (Villa Sofia farm)	NA	NA	*Amynthas gracilis*, *Dichogaster affinis*, *Dichogaster bolaui*, *Glossodrilus griseus*, *Perionyx excavatus*	5	1/4	Feijoo et al. (2018)
	Armenia, La Revancha (Bella Marina farm)	NA	NA	*Dichogaster saliens*, *Periscolex columbianus*	2	1/1	Feijoo et al. (2018)
	Quindío, Armenia, El Rhin	NA	NA	*Periscolex columbianus*	1	1/0	Feijoo et al. (2018)
	Quindío, Armenia, La India (La Ermita farm)	NA	NA	*Periscolex coreguaje*	1	1/0	Feijoo et al. (2018)
	Circasia, Barcelona Baja rural (Buenos Aires farm)	NA	NA	*Amynthas gracilis*, *Dichogaster saliens*, *Pontoscolex corethrurus*	3	0/3	Feijoo et al. (2018)
	Quindío, Armenia, La India (La Miranda farm)	NA	NA	*Dichogaster saliens*	1	0/1	Feijoo et al. (2018)
	Quindío, Armenia, La Patria	NA	NA	*Dichogaster saliens*	1	0/1	Feijoo et al. (2018)
Costa Rica	Cahuita	NA	NA	*Pontoscolex corethrurus*	ND	?/1	Lapied and Lavelle (2003)
Cuba	Boyeros	Organic	Monoculture	*Dichogaster affinis*, *Dichogaster bolaui*, *Onychochaeta elegans*, *Polypheretima elongata*, *Protozapotecia angelesae*	5	2/3	Martínez-Leiva (2002)
Guadeloupe (France)	Capesterre-Belle-Eau	NA	Monoculture	*Pontoscolex corethrurus*	ND	?/1	Lafont et al. (2007)
	Capesterre-Belle-Eau (Gloria Bas)	Conventional	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Capesterre-Belle-Eau (Source)	Conventional	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Capesterre-Belle-Eau (Bergerie)	Agroecological	Monoculture	*Pontoscolex corethrurus*, unknown sp. 2	2	?	Burac et al. (2018)
	Baillilf (Sextius)	Agroecological	Monoculture	*Pontoscolex corethrurus*, unknown sp.	2	?	Burac et al. (2018)
	Baillilf (Grand Canon)	Agroecological	Monoculture	*Pontoscolex corethrurus*, unknown sp. 3	2	?	Burac et al. (2018)
	Saint-Claude (Saut d'Eau)	Agroecological	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
India	Dakshina Kannada District (Belthangady)	NA	NA	*Hoplochaetella kempi*	ND	1/0	Siddaraju et al. (2013)
	Dakshina Kannada District (Mangalore)	NA	NA	*Konkadrilus bahli*	ND	1/0	Siddaraju et al. (2013)
	Dakshina Kannada District (Mangalore)	NA	NA	*Dichogaster affinis*	ND	0/1	Siddaraju et al. (2013)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
India	Dakshina Kannada District (Bantwal)	NA	NA	*Octochaetona parva*	ND	1/0	Siddaraju et al. (2010)
	Dakshina Kannada District (sites not detailed)	NA	NA	*Amynthas corticis*, *Hoplochaetella kempi*, *Hoplochaetella stuarti*, *Hoplochaetella suctoria*, *Megascolex konkanensis*, *Metaphire posthuma*, *Octochaetona paliensis*, *Octochaetona parva*	ND	7/1	Siddaraju et al. (2010, 2013)
	Kerala (Vellayambalam)	NA	NA	*Perionyx excavatus*, *Pontoscolex corethrurus*	2	0/2	Nair et al. (2007)
	Mizoram	NA	Monoculture	*Drawida nepalensis*, *Drawida rangamatiana*, *Drawida* sp., *Metaphire houlleti*, *Perionyx excavatus*	5	3/2	Lalthanzara (2007)
	Mizoram	NA	Polyculture	*Drawida nagana*, *Drawida* sp., *Metaphire houlleti*, *Perionyx excavatus*	4	2/2	Lalthanzara (2007)
	Rajapalayam	NA	NA	*Lampito mauritii*, *Perionyx excavatus*	2	1/1	Mariappan et al. (2013)
	Udupi District (Adve)	NA	NA	*Megascolex konkanensis*	1	1/0	Kumar et al. (2018)
	Udupi District (Adve)	NA	NA	*Metaphire houlleti*	1	0/1	Kumar et al. (2018)
	Udupi District (Bellibetu)	NA	NA	*Metaphire houlleti*, *Pontoscolex corethrurus*	2	0/2	Kumar et al. (2018)
	Udupi District (Mudarangadi)	NA	NA	*Pontoscolex corethrurus*	1	0/1	Kumar et al. (2018)
	Udupi District (Nandikur)	NA	NA	*Drawida ampullacea*, *Drawida sulcata*, *Metaphire peguana*	3	3/0	Kumar et al. (2018)
	Udupi District (Nandikur)	NA	NA	*Drawida ampullacea*	1	1/0	Kumar et al. (2018)
	Udupi District (Padabettu)	NA	NA	*Perionyx excavatus*	1	0/1	Kumar et al. (2018)
	Udupi District (Yellur)	NA	NA	*Mallehulla indica*, *Megascolex konkanensis*	2	2/0	Kumar et al. (2018)
	West Tripura (Mohanpur, Maheshkhola, Rastermatha)	Organic	Monoculture	*Amynthas alexandri*, *Drawida assamensis*, *Drawida papillifer*, *Eutyphoeus comillahnus*, *Lampito mauritii*, *Lennogaster* sp., *Metaphire houlleti*, *Metaphire posthuma*, *Octochaetona beatrix*, *Perionyx excavatus*, *Pontoscolex corethrurus*	3–7	4/7	Dhar and Chaudhuri (2018)
Indonesia	Bangkalan (Kamal, Burneh, Socah, Bypass)	NA	NA	*Amynthas robustus*, *Metaphire californica*, *Metaphire javanica*	ND	1/2	Budijastuti (2019)
	Bangkalan (Tanah Merah)	NA	NA	*Metaphire posthuma*	1	0/1	Budijastuti (2019)
	Bangkalan (Labang)	NA	NA	*Amynthas robustus*, *Metaphire javanica*, *Metaphire californica*, *Pheretima racemosa*	4	2/2	Budijastuti (2019)
	Gresik (Driyorejo, Kedamean, Ngipik, SumengkoLegundi)	NA	NA	*Amynthas robustus*, *Metaphire javanica*	ND	1/1	Budijastuti (2019)
	Gresik (Wringinanamon)	NA	NA	*Amynthas robustus*, *Metaphire javanica*, *Metaphire posthuma*	3	1/2	Budijastuti (2019)
	Sidoarjo (Waru, Taman, Sidoarjo, Tulangan, Tanggulangin, Candi)	NA	NA	*Amynthas robustus*, *Metaphire javanica*, *Metaphire posthuma*	ND	1/2	Budijastuti (2019)
	Surubaya (Pakal, Benowo, Tandes, Sukolilo, Gubeng, Gununganyar)	NA	NA	*Amynthas robustus*, *Metaphire javanica*, *Metaphire posthuma*	ND	1/2	Budijastuti (2019)
Ivory Coast	Lamto region	NA	NA	*Dichogaster wenkei*, *Reginaldia anomala*, *Stuhlmannia palustris*, *Stuhlmannia zielae*	ND	4/0	Tondoh (1994)
Jamaica	Clarendon, Crofts Mountain	NA	NA	*Drawida barwelli*, *Polypheretima elongata*	2	0/2	Sims (1987)
Madagascar	Ambatosoratra Ambatondrazaka	NA	NA	*Kynotus sihanakus*, *Kynotus* sp.2	2	2/0	Razafindrakoto et al. (2016), Csuzdi et al. (2017)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Malaysia	Serdang, Sengalor (Universiti Putra Malaysia)	NA	NA	*Pontoscolex corethrurus*	ND	0/1	Teng et al. (2006)
Martinique (France)	Le Lorrain (Feugère)	Conventional	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Le Lorrain (Limite)	Agroecological	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Le Lorrain (Bellevue)	Conventional	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	L'Ajoupa-Bouillon (Allée Domergue 3)	Agroecological	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Basse-Pointe (Fromager Rivière)	Conventional	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
	Basse-Pointe (Dantu Bas)	Agroecological	Monoculture	*Pontoscolex corethrurus*	1	0/1	Burac et al. (2018)
Mexico	Tabasco	NA	Monoculture	*Lavellodrilus bonampakensis*, *Pontoscolex corethrurus*	2	1/1	Huerta et al. (2005)
	Tabasco, Teapa B1	NA	Monoculture	*Balanteodrilus pearsei*, *Drawida barwelli*, *Polypheretima elongata*, *Pontoscolex corethrurus*, *Pontoscolex* sp.	5	1/4	Geissen et al. (2009)
	Tabasco, Teapa B2	NA	Monoculture	*Balanteodrilus pearsei*, *Dichogaster bolaui*, *Drawida barwelli*, *Periscolex brachycystis*, *Polypheretima elongata*, *Pontoscolex* sp.	6	2/4	Geissen et al. (2009)
	Tabasco, Teapa AF1	Agroforestry	Polyculture	*Balanteodrilus pearsei*, *Dichogaster bolaui*, *Drawida barwelli*, *Polypheretima elongata*, *Pontoscolex corethrurus*, *Pontoscolex* sp.	6	2/4	Geissen et al. (2009)
	Tabasco, Teapa AF2	Agroforestry	Polyculture	*Balanteodrilus pearsei*, *Dichogaster bolaui*, *Drawida barwelli*, *Polypheretima elongata*, *Pontoscolex corethrurus*	5	1/4	Geissen et al. (2009)
	Tabasco, Teapa (site 1)	Conventional	NA	*Dichogaster saliens*, *Diplotrema murchiei*, *Pontoscolex corethrurus*	3	½	Huerta et al. (2013)
	Tabasco, Teapa (site 2)	Conventional	NA	*Dichogaster saliens*, *Pontoscolex corethrurus*	2	0/2	Huerta et al. (2013)
	Tabasco, Teapa (site 3)	Conventional	NA	*Diplotrema murchiei*, *Polypheretima elongata*, *Pontoscolex corethrurus*	3	1/2	Huerta et al. (2013)
	Tabasco, Teapa (site 4)	Conventional	Polyculture	*Amynthas gracilis*, *Pontoscolex corethrurus*	2	0/2	Huerta et al. (2007)
	Tabasco, Teapa (site 5)	Conventional	Polyculture	*Dichogaster saliens*, *Polypheretima elongata*, *Pontoscolex corethrurus*	3	0/3	Huerta et al. (2013)
	Tabasco, Teapa (site 6)	Conventional	NA	*Dichogaster saliens*, *Pontoscolex corethrurus*	2	0/2	Huerta et al. (2007)
	Tabasco, Pablo L. Sidar	NA	Monoculture	*Lavellodrilus bonampakensis*, *Pontoscolex corethrurus*	2	1/1	Huerta et al. (2013)
	Tamaulipas (Biosphere Reserve "El Cielo")	NA	NA	*Amynthas gracilis*	ND	0/1	Barois (1992)
	Actopan, Ejido Buenavista	NA	NA	*Balanteodrilus psammophilus*	ND	1/0	Fragoso and Rojas (2007)
Nicaragua	Managua	NA	NA	*Dichogaster bolaui*, *Periscolex brachycystis*	2	1/1	Sherlock et al. (2011)
Peru	Sarita Colonia	NA	Monoculture	*Pontoscolex corethrurus* and two native spp.	3	2/1	Pashanasi (2007)
Philippines	Davao (Sumitomo Fruits Corporation, 15% site)	Conventional	Monoculture	*Metaphire* sp., *Pithemera bicincta*, *Pontoscolex corethrurus*	3	1/2	Fusilero et al. (2013)
	Davao (Sumitomo Fruits Corporation, 25% site)	Conventional	Monoculture	*Metaphire cai*, *Metapheretima* sp., *Perionyx excavatus*	3	2/1	Fusilero et al. (2013)
Portugal	Madeira Island (Ribeira Brava)	NA	NA	*Aporrectodea moebii*, *Eisenia eisensi*, *Metaphire californica*	3	0/3	Talavera (1996)
	Madeira Island (Funchal)	NA	NA	*Amynthas gracilis*, *Metaphire californica*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1996)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Portugal	Madeira Island (Santa Cruz)	NA	NA	*Amynthas gracilis*	1	0/1	Talavera (1996)
	Madeira Island (Terceira Lombada)	NA	NA	*Aporrectodea moebii*, *Eiseniella tetraedra*	2	0/2	Talavera (1996)
	Madeira Island (Porto Moniz)	NA	NA	*Amynthas gracilis*, *Aporrectodea rosea*, *Aporrectodea trapezoides*, *Dendrobaena pseudohortensis*	4	0/4	Talavera (2011)
	Madeira Island (Terceira Lombada)	NA	NA	*Aporrectodea caliginosa*, *Aporrectodea rosea*, *Eiseniella tetraedra*	3	0/3	Talavera (2011)
Seychelles	Cousine Island	NA	Monoculture	*Pontoscolex corethrurus*	ND	0/1	Plisko (2001)
South Africa	KwaZulu-Natal (Fairfield Farm)	NA	Monoculture	*Pontoscolex corethrurus*	ND	0/1	Plisko (2001)
	KwaZulu-Natal (Benhurst Farm)	NA	Monoculture	*Pontoscolex corethrurus*	ND	0/1	Plisko (2001)
	KwaZulu-Natal (6 sites in Eshowe)	NA	Monoculture	*Amynthas corticis*, *Amynthas minimus*, *Amynthas rodericensis*, *Dichogaster bolaui*, *Pontoscolex corethrurus*, and one other sp.	ND	0/5	Dlamini and Haynes (2004)
Spain	Gomera Island (Agulo)	NA	NA	*Amynthas rodericensis*, *Allolobophora chlorotica*, *Eiseniella tetraedra*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (1990a, 2007)
	Gomera Island (Barranco de la Villa)	NA	NA	*Bimastos rubidus*, *Ocnerodrilus occidentalis*, *Pithemera bicincta*	3	0/3	Talavera (2007)
	Gomera Island (Barranco del Valle)	NA	NA	*Allolobophora chlorotica*, *Metaphire californica*	2	0/2	Talavera (1990b, 2007)
	Gomera Island (Casas de Aluce)	NA	NA	*Aporrectodea rosea*, *Microscolex phosphoreus*	2	0/2	Talavera (2007)
	Gomera Island (Cabo Verde)	NA	NA	*Amynthas gracilis*, *Bimastos rubidus*	2	0/2	Talavera (1990b, 2007)
	Gomera Island (Costa Agulo)	NA	NA	*Aporrectodea trapezoides*, *Amynthas rodericensis*, *Bimastos rubidus*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (2007)
	Gomera Island (El Molinito)	NA	NA	*Amynthas morrisi*, *Microscolex phosphoreus*	2	0/2	Talavera (2007)
	Gomera Island (Hermigua)	NA	NA	*Aporrectodea rosea*, *Bimastos rubidus*, *Eisenia fetida*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (1990a, 2007)
	Gomera Island (Laguna de Santiago)	NA	NA	*Amynthas morrisi*, *Aporrectodea rosea*, *Aporrectodea trapezoides*, *Bimastos rubidus*, *Dendrobaena hortensis*, *Dichogaster affinis*, *Metaphire californica*, *Pithemera bicincta*	9	0/9	Talavera (2007)
	Gomera Island (Playa de Santiago)	NA	NA	*Ocnerodrilus occidentalis*	1	0/1	Talavera (1990a)
	Gomera Island (Seimal)	NA	NA	*Eiseniella tetraedra*, *Metaphire californica*, *Microscolex phosphoreus*	3	0/3	Talavera (2007)
	Gomera Island (Taguluche)	NA	NA	*Amynthas morrisi*, *Allolobophora chlorotica*, *Octalasion lacteum*	3	0/3	Talavera (2007)
	Gomera Island (Valle Gran Rey)	NA	NA	*Allolobophora chlorotica*, *Aporrectodea trapezoides*, *Dendrobaena hortensis*, *Eisenia fetida*, *Microscolex dubius*, *Pithemera bicincta*	5	0/5	Talavera (2007)
	Gran Canaria (Lomo del Galeón)	NA	NA	*Ocnerodrilus occidentalis*	1	0/1	Talavera (1990a)
	Gran Canaria (Los Llanos)	NA	NA	*Ocnerodrilus occidentalis*, *Pithemera bicincta*	2	0/2	Talavera (1990a)
	Gran Canaria Island (Bañaderos)	NA	NA	*Metaphire californica*	1	0/1	Talavera (1990b)
	Gran Canaria Island (Barranco Guiniguada)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)
	Gran Canaria Island (Frontón)	NA	NA	*Amynthas gracilis*	1	0/1	Talavera (1990b)
	Gran Canaria Island (Galdar)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Spain	Gran Canaria Island (Hoya Mondondo)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	Gran Canaria Island (La Aldea)	NA	NA	*Dichogaster affinis*	1	0/1	Talavera (1992b)
	Gran Canaria Island (Pedrazo)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	Gran Canaria Island (Tenoya)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)
	Hierro Island (Los Mocanes)	NA	NA	*Ocnerodrilus occidentalis*	1	0/1	Talavera (1990a)
	Hierra Island (NE tip)	NA	NA	*Microscolex phosphoreus*	ND	0/1	Talavera and Pérez (2009)
	La Palma Island (Barranco de las Angustias)	NA	NA	*Amynthas gracilis*	1	0/1	Talavera (1990b)
	La Palma Island (Barranco Nogales)	NA	NA	*Amynthas gracilis*	1	0/1	Talavera (1990b)
	La Palma Island (El Socorro)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	La Palma Island (La Caldereta)	NA	NA	*Amynthas morrisi*, *Metaphire californica*	2	0/2	Talavera (1990b)
	La Palma Island (Los Cancajos)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)
	La Palma Island (Los Llanos de Aridane)	NA	NA	*Amynthas morrisi*, *Metaphire californica*	2	0/2	Talavera (1990b)
	La Palma Island (Tazacorte)	NA	NA	*Amynthas gracilis*, *Amynthas morrisi*, *Metaphire californica*	3	0/3	Talavera (1990b)
	Tenerife Island (Abama)	NA	Monoculture	*Aporrectodea rosea*, *Dendrobaena hortensis*, *Eisenia andrei*, *Microscolex dubius*	4	0/4	Talavera (1992a)
	Tenerife Island (Adeje)	NA	NA	*Ocnerodrilus occidentalis*	1	0/1	Talavera (1990a)
	Tenerife Island (Bajamar)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Dichogaster affinis*, *Eisenia andrei*, *Microscolex phosphoreus*, *Ocnerodrilus occidentalis*	6	0/6	Talavera (1990a, 1992a, 1992b)
	Tenerife Island (Barranco de Santos)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Bimastos rubidus*, *Eisenia andrei*, *Microscolex dubius*, *Pithemera bicincta*	6	0/6	Talavera (1990b, 1992a)
	Tenerife Island (Barranco del Inglés)	NA	Monoculture	*Aporrectodea rosea*, *Aporrectodea trapezoides*, *Eisenia andrei*, *Microscolex dubius*	4	0/4	Talavera (1992a)
	Tenerife Island (Barranco la Atalaya)	NA	Monoculture	*Aporrectodea rosea*, *Pithemera bicincta*	2	0/2	Talavera (1992a)
	Tenerife Island (Barranco las Galletas)	NA	Monoculture	*Aporrectodea rosea*, *Eisenia andrei*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1992a)
	Tenerife Island (Barranco San Felipe)	NA	Monoculture	*Amynthas gracilis*, *Eisenia andrei*, *Pithemera bicincta*	3	0/3	Talavera (1992a, 1990b)
	Tenerife Island (Buenavista del Norte)	NA	NA	*Ocnerodrilus occidentalis*	1	0/1	Talavera (1990a)
	Tenerife Island (Casablanca)	NA	Monoculture	*Amynthas corticis*, *Aporrectodea rosea*, *Eisenia andrei*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (1992a)
	Tenerife Island (Costa Valle Guerra)	NA	Monoculture	*Amynthas gracilis*	1	0/1	Talavera (1992a)
	Tenerife Island (El Puente)	NA	Monoculture	*Amynthas gracilis*, *Aporrectodea rosea*, *Eisenia andrei*, *Microscolex phosphoreus*, *Ocnerodrilus occidentalis*	5	0/5	Talavera (1992a)
	Tenerife Island (El Rincón)	NA	Monoculture	*Amynthas gracilis*, *Bimastos rubidus*, *Dendrobaena cognetti*, *Microscolex dubius*, *Microscolex phosphoreus*, *Octodrilus complanatus*	6	0/6	Talavera (1992a)

Country	Location	Management	Culture type	Earthworm species	Richness	Native (N) / Exotic (E)	References
Spain	Tenerife Island (El Socorro)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	Tenerife Island (Fañabé)	NA	Monoculture	*Amynthas corticis*, *Aporrectodea rosea*, *Dichogaster affinis*, *Eisenia andrei*, *Ocnerodrilus occidentalis*	5	0/5	Talavera (1990a, 1992a, 1992b)
	Tenerife Island (Güimar)	NA	NA	*Dichogaster affinis*, *Ocnerodrilus occidentalis*	2	0/2	Talavera (1990a, 1992b)
	Tenerife Island (Iboybo)	NA	Monoculture	*Aporrectodea rosea*, *Eisenia andrei*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1992a)
	Tenerife Island (Icod de Los Vinos)	NA	Monoculture	*Dendrobaena cognetti*, *Bimastos rubidus*, *Octodrilus complanatus*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (1992a)
	Tenerife Island (Igueste)	NA	Monoculture	*Allolobophora chlorotica*, *Aporrectodea rosea*, *Aporrectodea trapezoides*, *Pontoscolex corethrurus*, *Ocnerodrilus occidentalis*	5	0/5	Talavera (1992a)
	Tenerife Island (La Hondura)	NA	Monoculture	*Amynthas morrisi*	1	0/1	Talavera (1992a)
	Tenerife Island (La Longuera)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Eisenia fetida*, *Microscolex dubius*, *Octodrilus complanatus*	5	0/5	Talavera (1992a)
	Tenerife Island (La Matanza)	NA	Monoculture	*Bimastos rubidus*, *Eisenia andrei*, *Microscolex phosphoreus*	3	0/3	Talavera (1992a)
	Tenerife Island (La Montañeta)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	Tenerife Island (La Vera)	NA	Monoculture	*Bimastos rubidus*, *Eisenia andrei*, *Microscolex phosphoreus*	3	0/3	Talavera (1992a)
	Tenerife Island (Las Arenas)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)
	Tenerife Island (Las Galletas)	NA	Monoculture	*Eisenia andrei*, *Bimastos eiseni*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1990a, 1992a)
	Tenerife Island (Las Madrigueras)	NA	NA	*Amynthas morrisi*	1	0/1	Talavera (1990b)
	Tenerife Island (Los Quintos)	NA	Monoculture	*Dendrobaena cognetti*, *Bimastos rubidus*, *Microscolex phosphoreus*, *Pithemera bicincta*, *Ocnerodrilus occidentalis*	5	0/5	Talavera (1992a)
	Tenerife Island (Los Realejos)	NA	NA	*Pithemera bicincta*	1	0/1	Talavera (1990b)
	Tenerife Island (Los Rechazos)	NA	Monoculture	*Aporrectodea trapezoides*, *Bimastos rubidus*, *Eisenia fetida*, *Octodrilus complanatus*, *Pithemera bicincta*	5	0/5	Talavera (1992a)
	Tenerife Island (Los Silos)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Dichogaster affinis*, *Eisenia andrei*, *Ocnerodrilus occidentalis*	5	0/5	Talavera (1992a 1992b)
	Tenerife Island (Loss Llanos)	NA	Monoculture	*Amynthas morrisi*, *Bimastos rubidus*, *Eisenia andrei*, *Pithemera bicincta*	4	0/4	Talavera (1992a)
	Tenerife Island (Playa de las Aguas)	NA	Monoculture	*Amynthas morrisi*, *Eisenia andrei*, *Pithemera bicincta*	3	0/3	Talavera (1992a)
	Tenerife Island (Playa de San Juan)	NA	Monoculture	*Aporrectodea rosea*, *Dendrobaena hortensis*, *Bimastos rubidus*, *Eisenia andrei*	4	0/4	Talavera (1992a)
	Tenerife Island (Playa San Marcos)	NA	Monoculture	*Pithemera bicincta*, *Bimastos rubidus*, *Microscolex phosphoreus*	3	0/3	Talavera (1992a)
	Tenerife Island (Puertito de Gilimar)	NA	Monoculture	*Microscolex phosphoreus*, *Pithemera bicincta*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1992a)
	Tenerife Island (Puerto de Santiago)	NA	Monoculture	*Amynthas morrisi*	1	0/1	Talavera (1990b, 1992a)
	Tenerife Island (Punta del Hidalgo)	NA	Monoculture	*Amynthas gracilis*, *Ocnerodrilus occidentalis*	2	0/2	Talavera (1992a)
	Tenerife Island (San Andrés)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Microscolex phosphoreus*, *Ocnerodrilus occidentalis*	4	0/4	Talavera (1992a)
	Tenerife Island (San Bernardo)	NA	Monoculture	*Amynthas corticis*, *Amynthas morrisi*, *Aporrectodea rosea*, *Eisenia andrei*	4	0/4	Talavera (1992a)

Country	**Location**	**Management**	**Culture type**	**Earthworm species**	**Richness**	**Native (N) / Exotic (E)**	**References**
Spain	Tenerife Island (San Juan de la Rambla)	NA	Monoculture	*Amynthas gracilis*, *Bimastos rubidus*, *Dendrobaena hortensis*, *Eisenia fetida*, *Pithemera bicincta*	5	0/5	Talavera (1990b, 1992a)
	Tenerife Island (San Pedro de Daute)	NA	Monoculture	*Amynthas morrisi*, *Aporrectodea rosea*, *Ocnerodrilus occidentalis*	3	0/3	Talavera (1992a)
	Tenerife Island (Santo Domingo)	NA	Monoculture	*Dendrobaena cognetti*, *Microscolex dubius*, *Microscolex phosphoreus*	3	0/3	Talavera (1992a)
	Tenerife Island (Taganana)	NA	Monoculture	*Amynthas morrisi*	1	0/1	Talavera (1992a)
	Tenerife Island (Tejina)	NA	Monoculture	*Amynthas corticis*, *Pithemera bicincta*	2	0/2	Talavera (1992a)
Taiwan	Central region	NA	NA	*Pontoscolex corethrurus*	ND	0/1	Tsai et al. (2000)
Uganda	Kabanyolo University Farm	NA	NA	*Dichogaster* sp. 1, *Dichogaster* sp. 2, *Gordiodrilus* sp., *Pygmaeodrilus* sp., *Polytoreutus* sp. 1	5	5/0	Block and Banage (1968)

Table 5. Number of quantitative (with abundance data) and qualitative (where species were identified) sampling sites and earthworm species (total, native, and exotic) and families found in banana plantations in different countries of the world.

Country	No. sites: Quant./Qual.[1]	Total No. species	Native	Exotic	Families
Asia	**6/≥47**	**35**	**22**	**13**	**5**
Bangladesh	0/1	3	1	2	2
China	0/1	1	0	1	1
India	4/≥20	27	20	7	5
Indonesia	0/23	5	1	4	1
Malaysia	0/1	1	0	1	1
Philippines	2/2	6	3	3	2
Taiwan	0/1	1	0	1	1
Africa	**33/97**	**50**	**20**	**30**	**7**
Cameroon	10/2	12	9	3	3
Canary Islands (Spain)[2]					
Gomera	0/13	18	0	18	4
Gran Canaria	0/10	6	0	6	3
Hierro	0/2	2	0	2	2
La Palma	0/7	3	0	3	1
Tenerife	0/45	19	0	19	5
Ivory Coast	1/1	4	4	0	3
Madagascar	0/1	2	2	0	1
Madeira (Portugal)[2]	0/6	10	0	10	3
Seychelles	0/1	1	0	1	1
South Africa	6/8	5	0	5	3
Uganda	6/1	5	5	0	3
North America	**12/16**	**14**	**7**	**7**	**4**
Bermuda	0/2	2	0	2	1
Mexico	12/14	12	5	7	4
Central America/Caribbean	**53/≥17**	**≥10**	**4**	**≥6**	**4**
Costa Rica	≥5/1	1	0	1	1
Cuba	1/1	5	2	3	3
Dominica	1/0	2	1?	1	2
Guadeloupe (France)	40/7	4?	?	≥1	≥1
Martinique (France)	6/6	1	0	1	1
Jamaica	0/1	2	0	2	2
Nicaragua	0/1	2	1	1	2
South America	**49/33**	**20**	**10**	**10**	**6**
Brazil	16/16	7	0	7	5
Colombia	32/15	15	8	7	4
Peru	1/1	3	2	1	≥1
Total	**153/210**	**≥104**	**≥61**	**≥43**	**10**

[1]Quant.=quantitative samples, taken using various sampling methods (mostly hand sorting of soil monoliths); Qual.=qualitative samples, usually performed for biodiversity studies (species presence) and normally without specifying volume of soil sampled; [2]Although politically these islands belong to Europe, biogeographically they belong to Africa.

Table 4), the role of less intensive banana production systems in maintaining native earthworm populations must still be further evaluated.

High species richness was also detected overall in Spain (25), mainly due to the higher sampling effort involving a large number of sites in the Canary Islands. However, all of the species encountered on the islands offshore of Africa were exotic, their introduction having been stimulated over centuries of human colonization bringing in exotic soils and crops (Talavera 2007, 2011). The Caribbean islands had few species (5), despite a large sampling effort, and many sites were dominated by *P. corethrurus* (Burac et al. 2018). In Brazil, Costa Rica, Martinique, Jamaica, Bermuda, the Seychelles, Taiwan, Malaysia, and China, all the earthworm species encountered were exotic (Table 5). The continent with the highest number of species recorded was Africa (50), of which 40% were native. In Asia, 35 species were recorded, with a higher proportion of natives (66%). In North and South America, around 50% of the species found were native, but these were mainly due to the higher number of natives observed in Colombian (Feijoo et al. 2018) and Mexican (Geissen et al. 2009; Huerta et al. 2013) plantations.

Species richness in individual banana/plantain fields was measured in 166 of the 210 sites, and was generally very low, with an overall mean of 2.7 species per site worldwide, of which less than one (0.5) was native and 2.1 were exotic (full dataset in Cremonesi et al. 2020). Absolute richness in an individual plantation was highest in the banana plantations in Cameroon (Norgrove et al. 2011), where 8 and 10 species were found (Table 4), most of them native. The only other place with such high richness was a plantation in Gomera Island (Laguna de Santiago), where 9 species were found (Talavera 2007), although all of them were exotic. In West Tripura, up to 7 species were found in a banana plantation (Dhar and Chaudhuri 2018), but most plantations in the world had less than 3 species (~70% of sites), and the highest proportion was of sites with only 1 species (~30% of sites).

There was a clear positive relationship between the number of sites sampled in each country and the total number of species encountered ($r = 0.7$, $p< 0.01$), particularly for exotic ($r = 0.78$, $p < 0.01$) species (Fig. 3A). Although also positive, this relationship was not significant for native species. Nonetheless, the species accumulation curve for native species for all sampling sites in the world revealed a steep slope, that contrasts with the flattened-out accumulation curves for total and exotic species (Fig. 3B). This indicates that greater sampling efforts, particularly in more low-input production systems, especially in tropical countries with high earthworm biodiversity such as Ecuador (no studies with earthworms identified yet), Brazil and Colombia (Brown and James 2007; Feijoo 2007; Zicsi 2007) will certainly increase the number of species known from banana/plantain fields. Greater sampling efforts are also needed in other tropical countries with important plantain/banana production (FAO 2018), particularly when intercropped or in agroforestry systems (Norgrove et al. 2011; Norgrove and Hauser 2014), and where mostly native earthworm species may inhabit these fields, such as seen for Cameroon, Uganda and Ivory Coast. This phenomenon may likely also be applicable to other Western, Central and Eastern African countries, as well as many other Asian and Pacific countries, but the paucity of available data impedes further speculation.

Of the over 100 species found in banana and plantain fields worldwide, most belonged to the Megascolecidae (22%), Lumbricidae (17%) and Acanthodrilidae (16%) families (Cremonesi et al. 2020). These widespread exotic and often invasive species are found throughout the tropics and subtropics, and include several *Amynthas* and *Metaphire* spp. (Blakemore 2002). The most consistently recorded megascolecids were *A. gracilis* (6% of all records), *Amynthas morrisi* (Beddard, 1892) (5%), *Pithemera bicincta* (Perrier, 1875) (4%) and *Metaphire californica* (Kingerg, 1867), *Perionyx*

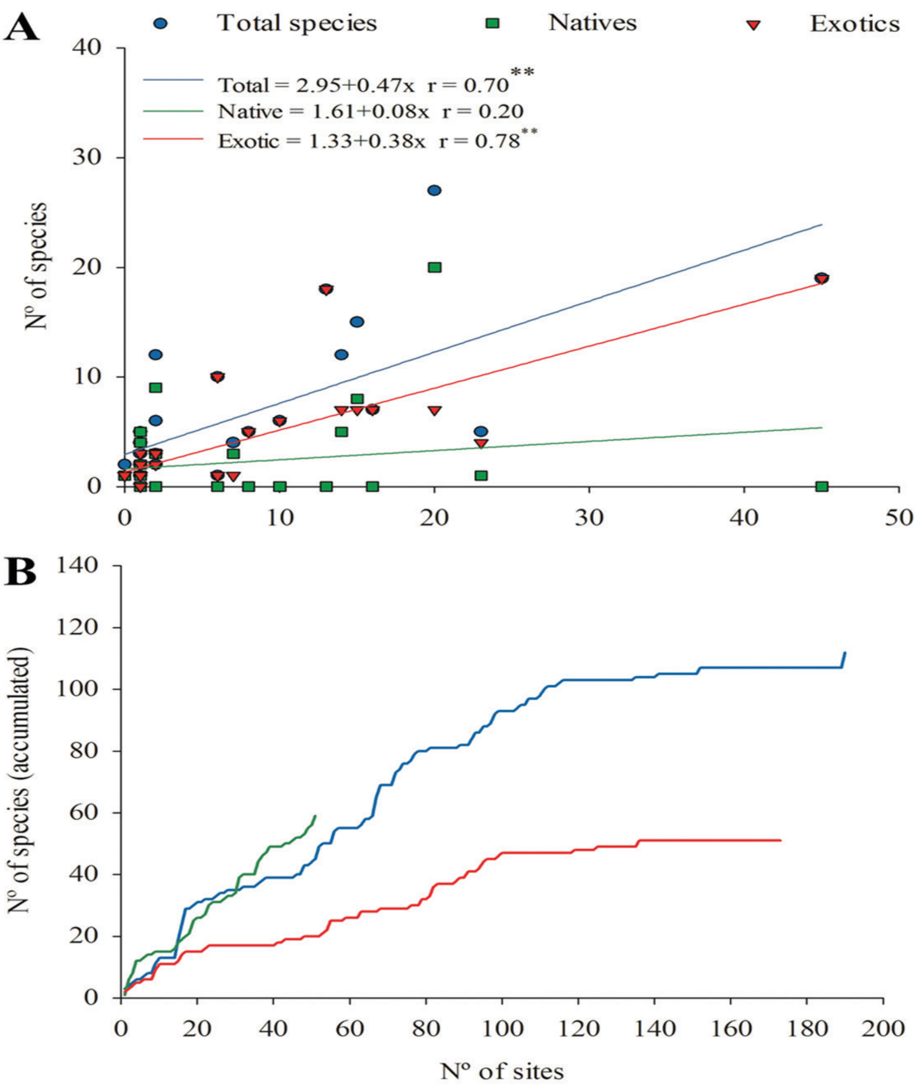

Figure 3. A Relationship between species richness (total, native, and exotic species) and the number of sampling sites in each world country (data from Table 5) and **B** Species accumulation curves for total, native and exotic species, depending on the number of sampling sites across the world. Linear regression equations and the value and significance (p value, with ** indicating p< 0.01) of the Pearson correlation coefficient (r) are provided in (**A**).

excavatus Perrier, 1872 and *Polypheretima elongata* (Perrier, 1872) (all with 2% each) (Cremonesi et al. 2020). These megascolecids were found in over 15 countries, and were especially frequent in the Canary Islands. All of the lumbricids reported were exotic, and mainly found in the Canary and Madeira Islands (Spain, Portugal), with *Aporrectodea rosea* (Savigny, 1826) and *Eisenia andrei* Bouché, 1972 (both with ~4%)

and *Bimastos rubidus* (Savigny, 1826) (3%) being the most frequently reported. Various octochaetid *Dichogaster* spp. of the Benhamiinae subfamily, i.e., *Dichogaster* (*Diplothecodrilus*) *affinis* (Michaelsen, 1890), *D.* (*D.*) *bolaui* (Michaelsen, 1891) and *D.* (*D.*) *saliens* (Beddard, 1893) (all with around 2% each) and the acanthodrilinae *Microscolex* spp., i.e., *Microscolex phosphoreus* (Dugés, 1837) with 3% and *M. dubius* (Fletcher, 1887) with 2% of records, were the most reported acanthodrilids. The *Dichogaster* spp. were found in 11 countries, mainly in Latin America and the Canary Islands, while the *Microscolex* spp. were found only in the Canary Island banana plantations. Similarly, the ocnerodrilid *Ocnerodrilus occidentalis* Eisen, 1878 with 6% of all records, was found in three countries (Brazil, Portugal, Spain), but most frequently in the Canary Islands.

The most commonly encountered earthworm species in banana plantations was *P. corethrurus* (11%), found in 15 countries, mainly in Latin America, but also in places as far away as South Africa, India, Bangladesh, Malaysia, Philippines and Taiwan. Interestingly, 37 out of 54 sites (69%) that identified earthworm species reported *P. corethrurus* as dominant in the banana plantations (Table 3).

Although *P. corethrurus* may affect soil physical properties negatively by increasing soil compaction under some conditions, it can also positively affect biogeochemical processes, microbial activity, plant production, and soil recovery (see review in Taheri et al. 2018). Furthermore, this species is known to reduce plant-parasitic nematode incidence in banana plants (Loranger-Merciris et al. 2012), and has also been known to promote beneficial plant growth-promoting bacteria in the rhizosphere (Braga et al. 2015). Hence, further work is warranted on the potential beneficial impacts of the presence and populations of *P. corethrurus* on banana plants, particularly considering its widespread distribution and high abundance in some locations (e.g., Costa Rica, Brazil, Guadeloupe, Martinique, Mexico). Several megascolecids such as *A. gracilis* are also known to affect soil physical and chemical properties in annual cropping systems (e.g., Peixoto and Marochi 1996; Bartz et al. 2010) as well as crop production (Brown et al. 1999), but little is known of their effects on banana plants. The latter statement is also valid for all of the other species most commonly found in banana plantations.

A total of 31 studies performed in 153 sites and 15 countries (Table 5) had quantitative earthworm data (on abundance and/or biomass) taken mainly by hand sorting soil monoliths of variable size (mostly 25 x 25 cm but sometimes larger, e.g., 50 × 50 cm) and occasionally using liquid extraction (e.g., formalin expulsion). Most of the study sites were in Guadeloupe (*N* = 40, of which 34 were by Clermont-Dauphin et al. (2004) and Colombia (*N* = 32; Molina and Feijoo 2017).

Overall earthworm abundance ranged from a minimum of 0 (Figueroa 2019) in an Ecuadorian plantation, to a maximum mean of over 1500 indiv. m^{-2} in banana plantations in Kwazulu-Natal, South Africa (Dlamini and Haynes 2004). Maximum biomass attained was 453.6 g m^{-2} for a site in West Tripura, India (Dhar and Chaudhuri 2018). Interestingly, a large number of sites (>50) had abundance values over 100 indiv. m^{-2}, which could be considered quite high for earthworm density in annual agricultural crops (Bartz et al. 2013). Nonetheless, bananas are perennials often cultivated over several cropping cycles, allowing for reduced negative effects of soil preparation, and the soils are also often limed to correct pH and fertilized with inorganic fertilizers (mainly N, P and K) to promote soil fertility and banana production. In these conditions, earthworms present find a soil protected from rainfall impact, as well as frequent organic matter additions through the management of the banana trees, particularly where the residues are left on the soil surface. Consequently, their populations can increase rather rapidly over time, as observed by Okwakol (1994) in Uganda (Table 3).

These high earthworm abundances and biomasses may be contributing significantly to soil processes (bioturbation, nutrient cycling) in banana/plantain fields, as biomasses over 17 g m^{-2} and above 32 g m^{-2} are known to lead to moderate (20–40%) and important (>40%) grain production increases, respectively (Brown et al. 1999). Earthworm-induced improvement of plant health and production includes, e.g., plant-parasitic nematode population control (Lafont et al. 2007; Loranger-Merciris et al. 2012), high stable bioaggregate formation, creation of many galleries in the soil and enhanced nutrient mineralization (Lavelle 1997), all factors that deserve future attention. On the other hand, low earthworm abundance may be an indicator of soil degradation, or the use of inappropriate management practices, such as soil inversion or toxic pesticide use (Demetrio et al. 2019). This type of information could be used to help farmers with their management decisions, such as reduction in nematicide applications that reduce earthworm populations (Clermont-Dauphin et al. 2004).

Finally, 18 of the major banana-producing countries in the world (34 countries with >30,000 ha in production, or >1 Million T bananas produced yr^{-1}; FAO 2018) were not examined in the present review due to lack of data. Hence, further sampling efforts are needed in order to provide adequate information on earthworm abundance and biodiversity in banana plantations in these countries, and to complement those reported here but with low sample intensity, particularly focusing on the presence of native species and/or large earthworm abundances, and to identify the reasons for these phenomena and their consequences for banana production and biodiversity conservation.

Conclusions

Earthworms are an important component of banana and plantain fields worldwide and deserve further attention by taxonomists, ecologists and agronomists. Under some conditions, especially in lower-input polycultures, their abundance and biomass may reach high values and contribute significantly to soil processes and plant production. More than 70 studies performed in over 200 banana plantations of 28 countries found >100 species (around 60% of them native) from 10 families, although species richness in each sited tended to be low (generally <3 species) and exotic species predominated (particularly *P. corethrurus*). However, as many important banana-producing countries have not yet been evaluated, further work is warranted in order to better understand the earthworm communities and their functional roles in plantain/banana fields, and the role of management practices in affecting their populations and diversity worldwide.

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Morphological and genetic evidence supports the separation of two *Tapinoma* ants (Formicidae, Dolichoderinae) from the Atlantic Forest biome

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Abstract

The taxonomic boundaries of many Neotropical ant species of the genus *Tapinoma* are still unclear. *Tapinoma atriceps* and *T. atriceps breviscapum* are two morphologically similar taxa which occur sympatrically in the southern Atlantic Forest of Brazil. Some characters such as the scape length and head shape suggest that these taxa may be different species. We used DNA analysis and morphological evidence, including scanning electron microscopy, to evaluate the taxonomic validity of these taxa. We found distinct morphological characteristics that allow separating them as two different species, *Tapinoma atriceps* and *Tapinoma breviscapum* **status novo**, and this decision is supported by the DNA results, where *Tapinoma atriceps* was recovered as a lineage independent of *T. breviscapum*.

Keywords

Cryptic diversity, haplotype network, intraspecific variation, mitochondrial DNA, neglected taxon, phylogenetic reconstruction

Introduction

Tapinoma Foerster is an ant genus distributed worldwide, with 69 known species (Bolton 2021) mostly in the tropics. Of these 69 valid taxa, 19 species, including several undescribed ones, are recognized in the Neotropical region (R.J. Guerrero unpublished data). The workers are morphologically recognized by their small size and reduced petiolar node covered by the first gastral tergite (Shattuck 1992), although these characteristics are convergent with *Technomyrmex*. *Tapinoma* workers, however, can be differentiated from those of *Technomyrmex* in that the latter present five gastral tergites, while in *Tapinoma* only four tergites are present. *Tapinoma atriceps* Emery, 1888, which was was described as a pale-yellow ant with a brown head and gaster from specimens collected at an unknown locality in the state of Rio Grande do Sul (Brazil), is considered vaguely similar to *Tapinoma melanocephalum* (Fabricius, 1793). *Tapinoma atriceps breviscapum* Forel, 1908 was later described from specimens with a similar color pattern to *T. atriceps* and collected in the state of São Paulo, but it is recognizable by having a longer and more rectangular head and shorter scapes.

According to published records for Brazil, *T. atriceps* occurs in the states of Mato Grosso do Sul (Demetrio et al. 2017), Rio de Janeiro (Eidmann 1936; Santos et al. 2019), São Paulo (Forel 1908), Paraná (Lozovei 2001), Santa Catarina (Farneda et al. 2007; Lutinski et al. 2008, 2013; Schmid et al. 2010; Gadelha et al. 2016), and Rio Grande do Sul (Emery 1888). Outside of Brazil, *T. atriceps* has been reported from rainforest in Misiones, Argentina (Hanisch et al. 2015) and Canindeyú, Paraguay (Wild 2007a). These records show that it mainly inhabits vegetation of the Atlantic Forest in southeastern South America. In contrast with the many records of *T. atriceps*, there are no published records for *T. a. breviscapum* after its description, perhaps because of misidentifications with *T. atriceps*.

There is no recent taxonomic revision of *Tapinoma* nor a phylogenetic framework to understand the relationships among the Neotropical species of *Tapinoma*, nor DNA sequences for many species. Given this situation, the identity and boundaries of species like *T. atriceps*, as well as the validity of the subspecies *T. a. breviscapum*, are unclear. The integration of molecular data along with the examination of morphology could provide a clear resolution of taxonomic limits in these taxa. Here, we used morphological and DNA evidence to evaluate the taxonomic validity of *T. atriceps* and *T. atriceps breviscapum*.

Material and methods

We examined 180 specimens of *Tapinoma atriceps* and *T. a. breviscapum*, including workers, queens, and males. A syntype worker of *Tapinoma atriceps* was examined from high-resolution photographs available at http://www.antweb.org (specimen code CASENT0904029). Three syntype workers of *T. a. breviscapum* from the Museum d'Histoire Naturelle (**MHNG**) were also examined.

Institutional acronyms

The collection abbreviations are taken from Evenhuis (2020) except for those ones marked with an asterisk (*). The material upon which this study is based is located and/or was examined at the following collections or institutions:

ALWC	Alexander L. Wild personal collection, Austin, Texas, USA;
CPDC	Centro de Pesquisas do Cacau, Comissão do Plano de Lavoura, Itabuna, Bahia, Brazil;
DZUP	Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil;
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland;
MSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy;
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil;
PSWC	Philip S. Ward Collection, University of California, Davis, California, USA*;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA;
WEMC	William and Emma Mackay Collection, University of Texas, El Paso, Texas, USA*.

Sampling and geographic origin

To obtain fresh samples for DNA and morphological analyses, we collected specimens in five Brazilian localities in the states of Minas Gerais, Paraná, and Santa Catarina between April 2016 and June 2017. Additional ethanol-stored specimens from Rio Grande do Sul and Misiones (Argentina) were included (Table 1). Field collections were carried out by searching actively in the vegetation, opening hanging dry twigs and standing branches. These specimens are deposited in the DZUP. Fieldwork was approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Sistema de Autorização e Informação em Biodiversidade (SISBIO) (approval number 25948-3).

Measurement and indices definitions

Morphological descriptions and measurements of specimens were performed using a Nikon SMZ 740 binocular stereomicroscope equipped with a micrometer at magnifications of 96×. Morphometric characters were examined in workers, queens, and males. The following measurements and indices were used (all measurements expressed in millimeters):

Head length (HL): in full-face view, the length between the mid-point of the anterior margin of the clypeus to the mid-point of a line tangent to the posterior margin of the head.

Head width (HW): in full-face view, the maximum width between the lateral margins of the head including the eyes which are within the cephalic capsule. In males, HW is recorded above compound eyes.

Scape length (SL): the maximum length of the scape excluding the basal constriction.

Weber'S, length (WL): in lateral view of the mesosoma, greatest distance from the approximate inflection point, where the pronotum curves into the cervical shield, to the posterior basal angle of the metapleuron.

Cephalic index (CI): HW/HL×100.

Scape index (SI): SL/HL×100.

The syntype worker of *Tapinoma atriceps* was measured from high resolution photographs using the program ImageJ v. 1.3 (Schneider et al. 2012). In the results, the measurements are presented as the mean value, followed by the standard deviation, with the minimum and maximum values between parentheses. Morphological terminology for wings follows Yoshimura and Fisher (2011).

Photographic resources and distribution map

High-resolution photographs of the specimens were captured using a Leica MZ16 stereomicroscope with a Leica DFC 500 camera, and final images were generated with Leica LAS 3D viewer LAS Montage v. 4.7. Integument surface and pilosity were examined using scanning electron microscopy (SEM) images generated with a JEOL JSM 6360-LV microscope under low vacuum (12–18 Pa) and a voltage acceleration of 15kV. Figure plates were designed with InkScape v. 0.92 (available at http://www.inkscape.org).

The distribution map of the species was made with Quantum GIS v. 3.8 (QGIS Development Team 2017) using locality records of the examined material. The coordinate system used was UTM WGS84. When available, geographic coordinates were taken from the labels, otherwise, the coordinates were estimated using Google Maps by choosing a central point from the cited locality. For the final map composition, we used a polygon of the Atlantic Forest from the World Wild Fund (Olson et al. 2001). Biology information was extracted from literature, field observations, and label data.

Designation of type specimens

Lectotypes of *Tapinoma atriceps* and *Tapinoma breviscapum* were designated by taking a worker from the syntype series of each of these taxa. By affixing a single specimen as the name-bearing type of *T. atriceps* and a single specimen as the name-bearing type of *T. breviscapum* (Art. 74, ICZN 1999), it "permanently deprives all other specimens that were formerly syntypes of that nominal taxon of the status of syntype; those specimens then become paralectotypes" (Art. 74.1.3, ICZN 1999).

Statistical analysis

For evaluating possible relationships between morphometric characters in the workers of both taxa, especially those associated with the head, we constructed bivariate graphs (e.g., HL vs SL). Considering that the length and width of the head or the length of the scape appear to show variability between the workers and queens of *T. atriceps* and *T. atriceps breviscapum*, we analyzed the variability of HL, HW, SL, and WL between these two taxa using a parametric or a non-parametric comparison test, depending on the results of the Normality test of the data. For the latter, each of these morphometric characters were analyzed with a Shapiro-Wilks test. For the worker data set (n = 44), only SL showed normality (W = 0.94, p = 0.0875, α = 0.05; Suppl. material 1: Table S1), while for queens only SL and HW showed normality (Suppl. material 1: Table S1), although this last result may be biased by the small number of samples (n = 10). None of the measurements in the males showed normality. The variability of these morphometric traits (i.e., non-overlapping differences) in workers and queens were analyzed using the Student's, t-test (T) with different sample sizes and different variances at a significance level of α = 0.05. In measurements with no normality, the difference of the two samples was evaluated with a Wilcoxon signed rank test at a significance level of α = 0.05. In the latter case, statistically significant differences were never found for any of the castes. All statistical analyses were performed in InfoStat v. 2020 (Di Rienzo et al. 2020).

DNA extraction, amplification, and sequencing

DNA was extracted, amplified, and sequenced from eight workers of *T. atriceps* from seven localities and one worker of *T. a. breviscapum* from one locality in the Serra do Cipó, Minas Gerais, which is the only colony we managed to collect. Unfortunately, all other studied samples of *T. a. breviscapum* were unsuitable for DNA extraction. DNA was extracted from entire specimens using a GenElute TM Blood Genomic Extraction Kit (Sigma-Aldrich, Darmstadt, Germany) following the kit instructions. From each sample one worker was conserved as a voucher (Table 1). Standard polymerase chain reaction (PCR) methods were used to amplify partial fragments of the mitochondrial gene Cytochrome c oxidase subunit I (COI), the nuclear genes Long-wavelength Rhodopsin (LW Rh) and *wingless* (Wg), and an exon-primed intron-crossing marker (EPIC). Primers can be found on Table 2.

DNA amplification was performed to a final volume of 25 µL. The PCR conditions for the COI marker were: 94 °C for 2 min, followed by 32 cycles of 94 °C for 45 s, 45 °C for 45 s, and 72 °C for 1 min, then 72 °C for 5 min. PCR conditions for Wg: 95 °C for 5 min, followed by 35 cycles of 92 °C for 1 min, 58 °C for 1 min, and 70 °C for 2 min, then 72 °C for 6 min. PCR conditions for the LW Rh marker: 95 °C for 5 min, followed by 35 cycles of 94 °C for 1 min, 56 °C for 1 min, and 70 °C for 1 min, then 72 °C for 5 min. PCR conditions for EPIC: 95 °C for 5 min, followed by 35 cycles of 92 °C for 1 min, 60 °C for 1 min, 70 °C for 1 min, then 72 °C for 6 min. All the sequences generated in this study were deposited in GenBank and the accession numbers are listed in Table 1.

Table 1. List of specimens used in phylogenetic reconstruction and haplotype network from molecular data. Geographic information for each of the samples is recorded. The GenBank codes of these specimens are also included.

Taxon	Country	State/province	Locality	Latitude/Longitude	Collection date	Voucher code	GenBank accession number				Haplotype code
							COI	LW Rh	WG	EPIC 1281	
Tapinoma atriceps	Argentina	Misiones	Parque Teyú Cuaré	27°10.248'S, 55°21.720W	28 Dec. 2007	DZUP 548801	MG920282	MN294972	-	-	H07
Tapinoma breviscapum	Brazil	Minas Gerais	Serra do Cipó	19°14.874'S, 43°33.054'W	25 Jun. 2017	DZUP 548800	MG920285	MN294973	MN294963	MT375619	H08
Tapinoma atriceps	Brazil	Minas Gerais	Serra do Cipó	19°15.264'S, 43°31.002W	26 Jun. 2017	DZUP 548799	MG920286	MN294971	MN294964	MT375620	H04
Tapinoma atriceps	Brazil	Paraná	Antonina	25°18.354'S, 48°39.678W	10-13 Jul. 2016	DZUP 548798	MG920278	MN294965	MN294957	MT375614	H01
Tapinoma atriceps	Brazil	Paraná	Antonina	25°17.796'S, 48°39.594'W	29 Oct. 2016	DZUP 548797	MG920280	MN294967	MN294959	-	H05
Tapinoma atriceps	Brazil	Paraná	Guaraqueçaba	25°09.816'S, 48°17.880'W	08 Oct. 2016	DZUP 548784	MG920281	MN294968	MN294960	MT375616	H06
Tapinoma atriceps	Brazil	Paraná	Paranaguá	25°35.016'S, 48°32.496'W	28 Apr. 2016	DZUP 548786	MG920279	MN294966	MN294958	MT375615	H02
Tapinoma atriceps	Brazil	Rio Grande do Sul	Porto Alegre	30°10.824'S, 51°06.078'W	27 Dec. 2016	DZUP 548788	MG920283	MN294969	MN294961	MT375617	H03
Tapinoma atriceps	Brazil	Santa Catarina	Florianópolis	27°35.928'S, 48°25.962'W	25 Feb. 2017	DZUP 548789	MG920284	MN294970	MN294962	MT375618	H01

Table 2. DNA primer sequences and references used for PCR amplification.

Genetic marker	Primer name	Sequence (5'–3')	Reference
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
COI	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
Wg	Wg578F	TGCACNGTGAARACYTGCTGGATGCG	Ward and Downie (2005)
Wg	Wg1032R	ACYTCGCAGCACCARTGGAA	Abouheif and Wray (2002)
LW Rh	LR143F	GACAAAGTKCCACCRGARATGCT	Ward and Downie (2005)
LW Rh	LR639ER	YTTACCGRTTCCATCCRAACA	Ward and Downie (2005)
EPIC 1281	ant.1281F	GACGCAGGTTGYAACGAAATCAC	Ströher et al. (2013)
EPIC 1281	ant.1281R	GCCRCTAATATCCAGCTTCACGAG	Ströher et al. (2013)

Analysis of genetic data

Consensus sequences were obtained with Staden Package (Staden 1996). The intronic region of LW Rh (LW Rhi) was separated and treated as a different marker than the exonic sequences (LW Rhe). For each marker, the sequences were aligned with Muscle (Edgar 2004) and then calculated nucleotide composition and *p*-distance in Mega X (Kumar et al. 2018). Composition for COI was analyzed by constructing a haplotype network using TCS network (Clement et al. 2002) in PopART v. 1.7 software (Leigh and Bryant 2015).

DNA sequences for the species *Tapinoma opacum* Wheeler & Mann, 1914 and *T. melanocephalum* (Fabricius, 1793) were downloaded from Genbank and used as outgroups (Suppl. material 2: Table S2). Of these taxa, *T. melanocephalum* was selected to root the phylogenetic tree as one phylogenetic analysis previous suggest that *T. opacum* and *T. atriceps* are nesting in a clade of Neotropical species which is sister to the Nearctic clade (*T. sessile* + *T. schreiberi*), while *T. melanocephalum* is phylogenetically distant from those clades (R.J. Guerrero unpublished data). For the phylogenetic analysis, each of the four aligned loci were analyzed separately in a Bayesian phylogenetic framework using MrBayes v. 3.2.6. Each of the three genes was divided by codon position (position 1 + 2 and 3), along with the LW Rh intron, which was treated as another partition for this gene. The partitions and the best substitution models used by MrBayes (Suppl. material 3: Table S3) were determined using Akaike information criterion (AIC) with PartitionFinder v. 2.1 (Lanfear et al. 2012). The concatenated alignment consisted of 2287 base pairs (bp) including the five markers. All phylogenetic analysis were performed with MrBayes through the CIPRES science gateway (Miller et al. 2010). The parameters of the Bayesian analysis consisted of two independent runs of ten million generations each, with four Markov chains sampled every 1000 generations (mcmc ngen = 10000000 relburnin=yes burninfrac=0.25 printfreq=1000 samplefreq=1000 nchains=4 savebrlens=yes; sump relburnin=yes; sumt relburnin=yes; contype=halfcompat;). Tracer v. 1.6 (Rambaut 2018) was used to visualize parameter estimates and ensure that all estimates converged prior to removing a burnin period of 1×10^6 generations. Convergence time among runs was determined as twice the number of generations it took the standard deviation of split frequencies to drop below 0.01.

Results

Species accounts

***Tapinoma atriceps* Emery, 1888**

Figs 1A, B, 2A, D, 3A, D, 4, 5

Tapinoma (*Micromyrma*) *atriceps* Emery, 1888: 363. Syntype series (several workers, queens, males): Brazil, Rio Grande do Sul (v. Ihering) [MSNG, AntWeb image of syntype examined]. One syntype worker (CASENT0904029) here designated lectotype.

Tapinoma atriceps Emery. Kempf 1972: 247.
Tapinoma atriceps Emery. Shattuck 1994: 142.
Tapinoma atriceps Emery. Bolton 2021: e-catalogue (http://antcat.org).

Worker diagnosis. Lateral margin of head in frontal view distinctly convex. Compound eye with 9 or 10 ommatidia along maximum diameter. Scape long (SI > 93). In profile, dorsal margin of propodeum forms distinct angle with propodeal declivity; dorsal margin short, about 1/4 length of declivitous margin (Fig. 4B).

Worker. Measurements (*n* = 26): HL 0.58 ± 0.04 (0.52–0.64), HW 0.50 ± 0.03 (0.42–0.55), SL 0.57 ± 0.04 (0.50–0.63), WL 0.69 ± 0.06 (0.60–0.78). Indices: CI 86 ± 3 (78–91), SI 97 ± 3 (93–103).

Head in full-face view oval, longer than wide, lateral margin convex, posterior margin slightly convex to straight (Fig. 1A). Maxillary palp relatively filiform, long, extending posteriorly beyond half of head. Masticatory margin of mandible with one large apical tooth, followed by two smaller teeth, fourth tooth larger than third, and then followed by denticles. Anterior margin of clypeus slightly emarginate medially. Scape almost as long as HL or greater (SI >93), surpassing posterior margin of head by distance equal to or greater than pedicel. In lateral view, dorsal margin continuously convex; metanotal groove weakly impressed; propodeum in lateral view slightly below level of mesonotum. Integument weakly imbricate, with exception of smooth petiole. Body covered by short, appressed pubescence. Head (excluding clypeus), antenna, and mesosoma lacking erect setae; clypeus with 6 long setae. Gastric tergites bearing erect hairs near their posterior margins: 2 hairs on first tergite, 2–4 on second, 4–6 on third, and 6–10 on fourth. Head and gaster medium brown; antennae, mesosoma, legs and petiole whitish yellow; mesosoma with brown spot on mesopleuron, spot sometimes present on lateroposterior corners of pronotum, metapleuron, and sides of propodeum.

Queen. Measurements (*n* = 4): HL 0.73 ± 0.03 (0.70–0.76), HW 0.68 ± 0.04 (0.64–0.71), SL 0.60 ± 0.02 (0.58–0.62), WL 1.23 ± 0.13 (1.08–1.32). Indices: CI 94 ± 3 (91–97), SI 83 ± 1 (82–83).

Head subquadrate in full-face view, slightly longer than broad (CI 91–97), lateral margin very convex, posterior margin straight to slightly convex (Fig. 2B). Mandibular masticatory margin with one large apical tooth, followed by 2 smaller teeth, fourth tooth larger than third, followed by 5 smaller teeth, and then small denticles decreasing in size. Anterior margin of clypeus slightly emarginate medially. Scape relatively long, reaching or surpassing posterior margin of head by length shorter than that of pedicel (SI 82–83). Forewing with crossveins 2r-rs, 2rs-m, and cu-a present (Fig. 2C, D). Hindwing with cu-a present, cubitus short, not projected after 1rs-m+M. Integument weakly imbricate; mesopleuron smooth. Body covered by short yellowish pilosity, excepting glabrous petiole. Clypeus bearing 6 long setae; gastric tergites each bearing several erect setae near their posterior margins. Body color medium brown; palps, flagella, coxae, trochanter, tibiae, tarsi, and petiole whitish yellow; propodeum usually brown, but sometimes with whitish-yellow spot on posterodorsal region. Gastric tergites I–III with pale-yellow, posterior transverse strip.

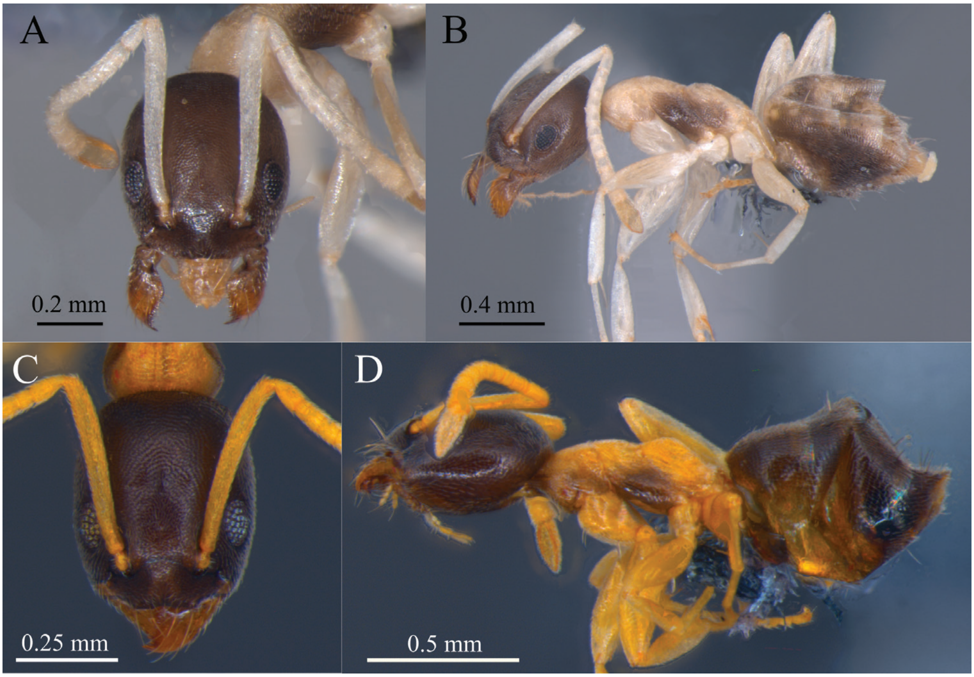

Figure 1. *Tapinoma atriceps* and *T. breviscapum* workers **A** head in frontal view of *T. atriceps* **B** body in lateral view of *T. atriceps* **C** head in frontal view of *T. breviscapum* **D** body in lateral view of *T. breviscapum*. Photographed specimens and those included in the molecular analyzes (haplotypes H04 and H08 respectively) are nestmates. Specimens deposited in DZUP. Photographs by M. Escárraga.

Male. Measurements (n = 4): HL 0.48 ± 0.04 (0.44–0.51), HW 0.52 ± 0.02 (0.50–0.53), SL 0.36 ± 0.04 (0.32–0.41), WL 0.63 ± 0.02 (0.61–0.66). Indices*:* CI 105 ± 11 (92–114), SI 76 ± 5 (71–82).

Head rounded in dorsal view; posterior margin slightly interrupted by posterior ocelli; anterior margin of clypeus straight to weakly emarginate medially. Eye large, rounded. Scape long, reaching or surpassing posterior head margin. Mandible semi-falcate; masticatory margin with large apical tooth followed by denticles of similar size forming a serrated surface continuing indistinctly up to the mandibular basal margin. Integument feebly imbricate, katepisternum smooth. On forewing, 1m-cu absent, median short. On hindwing, free section of radial and cu-a present, free section of cubitus absent. Row of long setae present on posterior margin of fore and hindwings. Head, scutum, and gaster covered by moderate, yellow, short, appressed hairs; scutellum glabrous. Hairs absent to scarce on pronotum, mesopleuron, propodeum, and petiole. Antenna covered by short, decumbent hairs. Gastric tergites I–V lacking erect setae. Head, mesosoma, petiole, and gaster dark brown. Antenna and legs light brown.

Distribution. *Tapinoma atriceps* occurs in Argentina, Brazil, and Paraguay (Fig. 5). In Argentina, this species is present in the northeastern corner of the country, in the province of Misiones. In Brazil, our records show the presence of this species in the

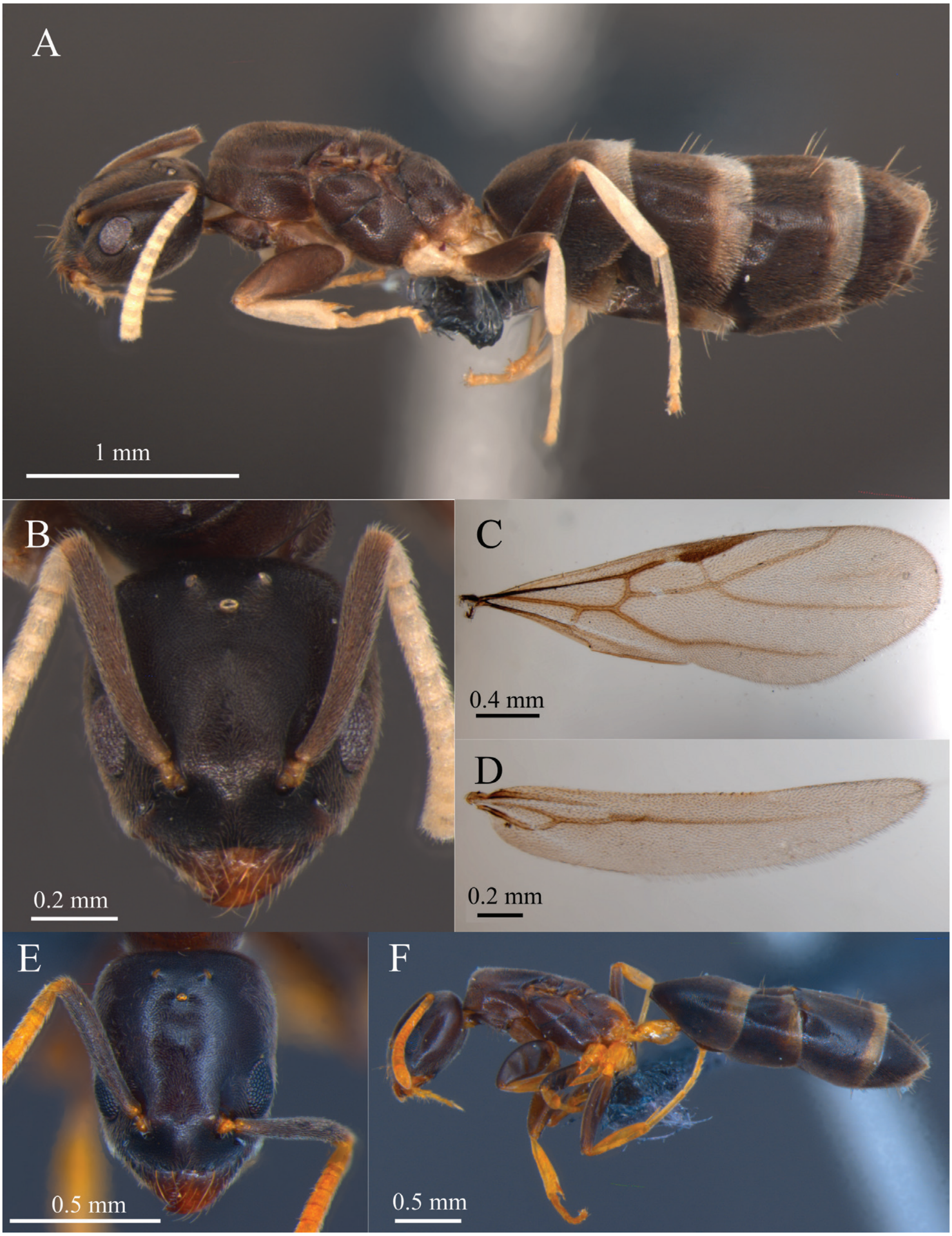

Figure 2. *Tapinoma atriceps* and *Tapinoma breviscapum* queen **A** body in lateral view of *T. atriceps* **B** head in frontal view of *T. atriceps* **C** anterior wing of *T. atriceps* **D** posterior wing of *T. atriceps* **E** head in frontal view of *T. breviscapum* **F** body in lateral view of *T. breviscapum*. Photographed specimens and those included in the molecular analyzes (haplotypes H04 and H08 respectively) are nestmates. Specimens deposited in DZUP. Photographs by M. Escárraga.

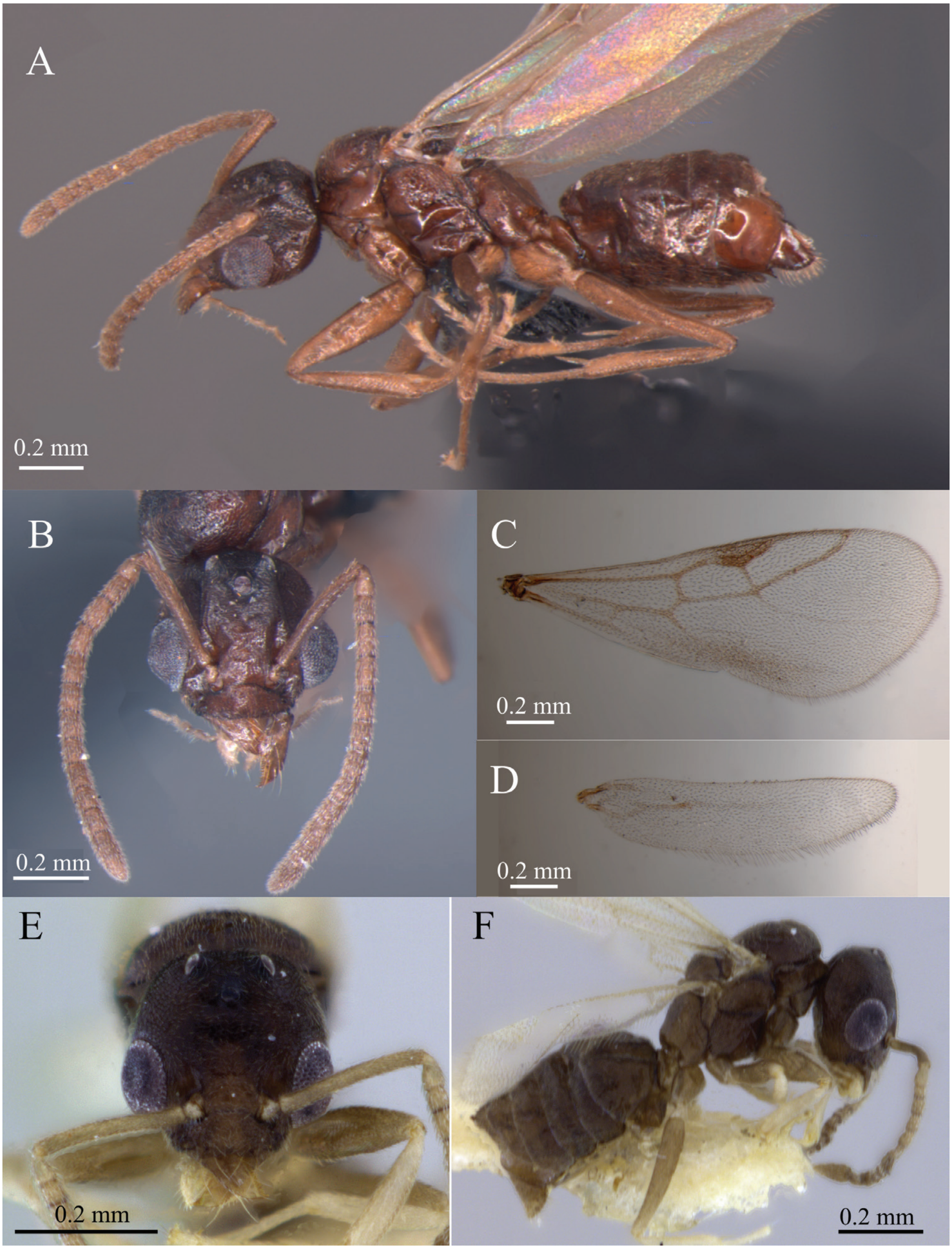

Figure 3. *Tapinoma atriceps* from Antonina, Reserva Natural Guaricica (Paraná, Brazil) and *T. breviscapum* from Serra do Cipó (Minas Gerais, Brazil) male **A** habitus of *T. atriceps* **B** head in frontal view of *T. atriceps* **C** anterior wing of *T. atriceps* **D** posterior wing of *T. atriceps* **E** head in frontal view of *T. breviscapum* **F** habitus of *T. breviscapum*. Specimens deposited in DZUP. Photographs by M. Escárraga.

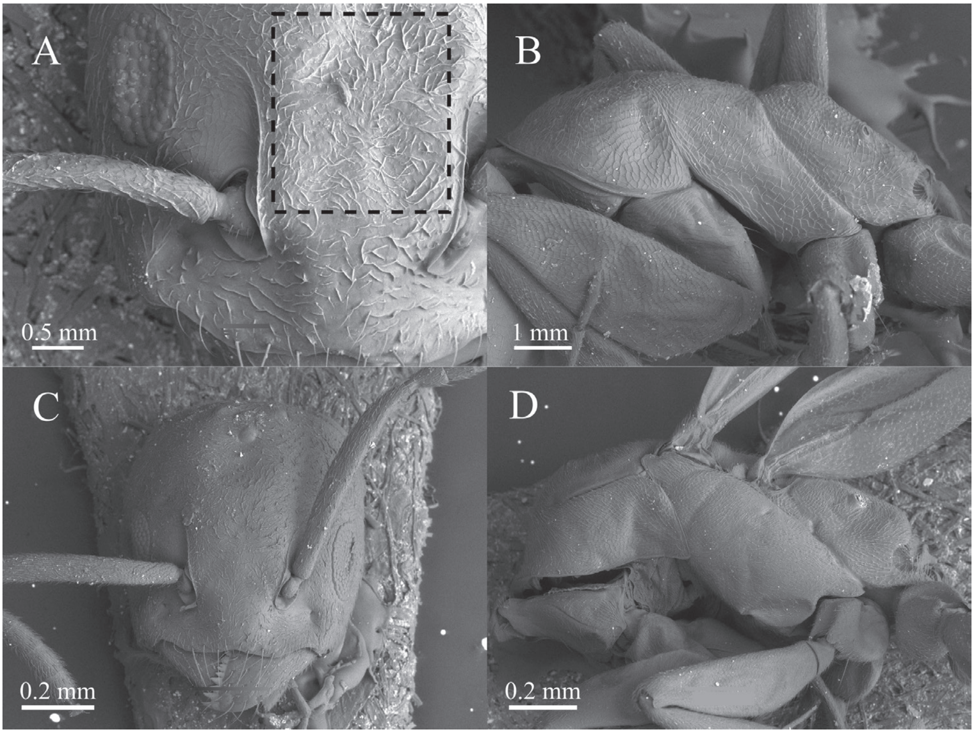

Figure 4. SEM microphotographs of *Tapinoma atriceps* from Serra do Cipó (Minas Gerais, Brazil) **A** worker head in dorsal view **B** worker mesosoma in lateral view **C** queen head in dorsal view **D** queen mesosoma in lateral view. The box with dashed lines indicates pubescence on the frons between the frontal carinae. Specimens deposited in DZUP.

states of Mato Grosso do Sul, Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, and São Paulo. In Paraguay, *T. atriceps* occurs in the department of Canindeyú.

Biology. *Tapinoma atriceps* is an arboreal ant which can be found from the understory layer to the canopy and rarely on the ground. We found nests of this ant in hollow cavities of the vegetation or dry hanging branches, in plants of the families Poaceae (Bambusoideae), Melastomataceae, Piperaceae, and Urticaceae. Workers are commonly found foraging on the leaves of plants near the nest. The colony can be moderately large, with more than 312 workers, and in a couple of nests we found four dealate queens, evidencing polygyny as in other species of *Tapinoma* (e.g., Bustos and Cherix 1998; Buczkowski and Bennet 2008).

Material examined. Argentina • 2 queens, 2 workers; Misiones, Parque Provincial Teyú Cuaré; 27°17.08'S, 55°35.62'W; 28 Dec. 2007; W. Mackay and E. Mackay legs; WEMC. BRAZIL • 1 worker; Mato Grosso do Sul, Dourados, Fazenda Azulão; 22°12.800'S, 54°55.133'W; 10 Mar. 2006; M. Santana and A.Vieira legs; DZUP • 2 males, 4 workers; Minas Gerais, Alto Caparaó, Parque Nacional Caparaó, 20°25.155'S, 41°51.083'W; 5–20 Dec. 2011; J. Chaul leg. DZUP • 1 worker; Minas Gerais, Lavras, Fragmento 06; Dec. 2002; M.S. Santos and N.S. Dias legs; CEPLAC

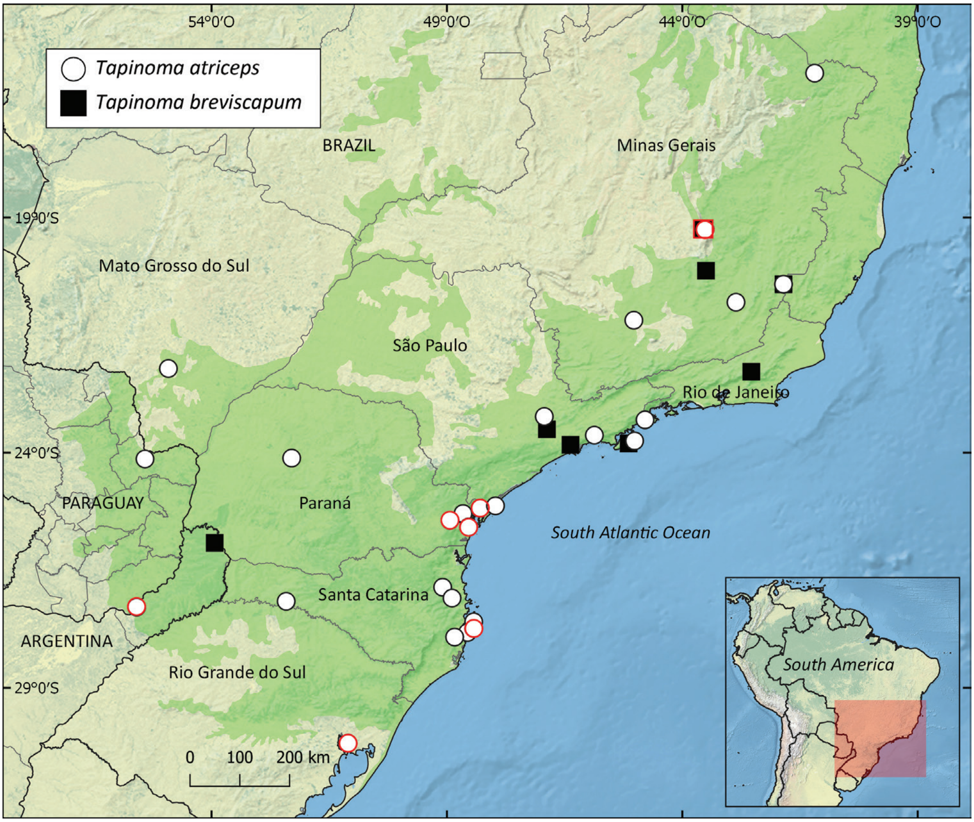

Figure 5. Distribution map of *Tapinoma atriceps* and *T. breviscapum*. The figures with red outline correspond to the localities for the sequenced specimens. Dark green area in the main map corresponds to the Atlantic Forest domain defined by the WWF.

• 1 queen; Minas Gerais, Pedra Azul; alt. 800 m; Nov. 1972, Seabra and Alvarenga legs; MZSP 10657 • 2 workers; Minas Gerais, Pedra Azul, Seabra and Alvarenga legs; MZSP 10658 • 1 worker, 1 queen; Minas Gerais, Serra do Cipó, 19°25.155'S, 43°51.083'W; 26 Ju. 2016; F. Siqueira leg.; DZUP • 1 worker; Minas Gerais, Viçosa, Mata do Paraíso; 1997/1998; S. de M. Soares leg.; CEPLAC • 1 male, 1 queen, 1 worker; Paraná, Antonina, Reserva Natural Guaricica, 25°17.794'S, 48°39.592'W; 26 Dec. 2016; C. da Costa leg.; DZUP • 1 queen, 1 worker; Paraná, Antonina, Reserva Natural Guaricica; 25°18.354'S, 48°39.678W; 29 Oct. 2016; M. Escárraga leg.; DZUP 548798 • 1 worker; Paraná, Antonina, Reserva Natural Guaricica; 10–13 Jul. 2016; M. Escárraga leg.; DZUP 548797 • 2 workers; Paraná, Guaraqueçaba, Reserva Natural Salto Morato, 25°09.816'S, 48°17.880'W; 8 Dec. 2016; M. Escárraga leg.; DZUP 548784 • 1 worker; Paraná, Paranaguá, Parque Estadual do Palmito; 25°35.016'S, 48°32.496'W, 28 Apr. 2016; M. Escárraga leg.; DZUP 548786 • 2 workers; Paraná, Pq. Marumby, Km 34, Estr. Graciosa; 3 Oct. 1980; A.L. Lozovei leg.; MZSP14069 • 1 worker; Rio Grande do Sul; MZSP11439 • 1 worker;

Rio Grande do Sul, Porto Alegre, Morro São Pedro, 30°10.824'S, 51°06.078'W; L. Kaminski leg.; DZUP • 2 workers; Rio Grande do Sul, Porto Alegre; 30°10.824'S, 51°06.078'W; 27 Dec. 2016; M. Escárraga leg.; DZUP 548788 • 3 workers; Santa Catarina, Blumenau; alt. 120 m;19 Jan. 1972; W.W. Kempf leg.; MZSP 7049 • 1 worker; Santa Catarina, Brusque, RPPN Chácara Edith; 27°05.692'S, 48°53.581'W; 28 Feb. 2013; Y. Gadelha leg.; DZUP • 1 worker; Santa Catarina, Florianópolis, Naufragados; 27°49.405'S, 48°33.694'W; 19 Feb. 2016; J. Chaul leg.; DZUP • 2 workers; Santa Catarina, Florianópolis; 27°35.928'S, 48°25.962'W; 25 Feb. 2017; M. Escárraga leg.; DZUP 548789 • 1 worker; Santa Catarina, Florianópolis, Praia Mole, 27°35.927'S, 48°25.962'W; 25 Feb. 2017; A. Menezes leg.; DZUP • 2 workers; Santa Catarina, Seara, Nova Teutônia; Jul. 1959; F. Plaumann leg.; MZSP • 1 worker; Santa Catarina, Seara, Nova Teutônia; 19 Dec. 1972; F. Plaumann leg.; MZSP8566 • 2 workers; Santa Catarina, Palhoça, Parque Estadual da Serra do Tabuleiro; 27°44.467'S, 48°41.833'W; 2–10 Jun. 2003; winkler 30; R.R. Silva, B. H. Dietz and A. Tavares legs.; MZSP • 3 workers; Santa Catarina, Seara, 24°07'S, 52°18'W; Jul. 1999; R. R. Silva leg.; Transecto II Isca Veget.; MZSP • 1 worker; Santa Catarina, Seara; Jul. 1958; F. Plaumann leg.; MZSP 2719 • 1 worker; Santa Catarina, Santo Amaro da Imperatriz, Parque Estadual da Serra do Tabuleiro, 27°55.356'S, 48° 50.277'W; 26 Nov. 2013; Y. Gadelha leg.; DZUP • 1 male, 1 queen, 1 worker; São Paulo, 8 Km SW Jundiaí; 23°14'S, 46°56'W; alt. 1180m,; 28 Dec. 1993; Manual; P.S. Ward leg.; [PSWC 12463] • 2 queens, 3 workers; São Paulo, Ilha da Vitória, 29 Mar.–6. Apr. 1965; Exp. Depto. Zool. legs; MZSP 4083 • 1 queen; São Paulo, Ilha da Vitória; 16–27 Mar. 1964; Exp. Depto. Zool. leg.; MZSP 4176 • 3 workers; São Paulo, Ilha da Vitória; 29 Mar.–6 Apr. 1966; Exp. Depto. Zool. leg.; MZSP 4117; • 2 workers; São Paulo, Ilha do Cardoso; Jan. 1979; Liliana Foneris leg.; MZSP • 2 workers; São Paulo, Salesópolis, Est. Biol. Boracéia; 11 Nov. 1960; K. Lenko leg.; MZSP 1788 • 4 workers; São Paulo, Salesópolis, Est. Biol. Boracéia; 13 Nov. 1960; K. Lenko leg.; MZSP 1483 • 1 worker; São Paulo, Salesópolis, Est.Biol. Boracéia, 3–5 May 1996; Brandão, Agosti, Diniz, Silvestre and Yamamoto legs; MZSP • 6 workers;São Paulo; USNM • 1 worker; São Paulo, Ubatuba, Parque Estadual Serra do Mar; 23°17.940'S, 44°47.220'W; 3–14 Mar. 2008; F. Esteves and R. Feitosa legs; MZSP • PARAGUAY. 1 worker; Canindeyú, Res. Nat. Bosque Mbaracayú, Jejuimí; alt. 107 m; 28 May–5 Jul.1996; Malaise; A.C.F. Costa leg.; ALWC.

Tapinoma breviscapum **Forel, 1908 status novo**

Figs 1C, D, 2E, F, 3E, F, 5, 6

Tapinoma atriceps breviscapa Forel, 1908: 384–385. Syntype series (worker, queen): Brazil, São Paulo, Raiz da Serra. [MHNG, examined]. One syntype worker (CASENT0909768) here designated lectotype; two workers designated as paralectotypes, uppermost specimen and lowermost on the same pin as lectotype worker (MHNG, examined).

Tapinoma atriceps breviscapum Forel. Kempf 1972: 247.
Tapinoma atriceps breviscapum Forel. Shattuck 1994: 142.
Tapinoma atriceps breviscapum Forel. Bolton 2021: e-catalogue (http://antcat.org).

Worker diagnosis. Lateral margin of head in frontal view slightly convex. Eye with 7 or 8 ommatidia along maximum diameter. Scape short (SI < 85). Dorsal face of propodeum in lateral view meeting propodeal declivity through rounded angle; length of dorsal margin about ½ that of declivity.

Worker. Measurements (*n* = 16): HL 0.58 ± 0.04 (0.53–0.66), HW 0.48 ± 0.04 (0.43–0.56), SL 0.48 ± 0.03 (0.44–0.56), WL 0.63 ± 0.06 (0.49–0.78). Indices: CI 83 ± 1 (82–85), SI 80 ± 2 (78–85).

Head in full-face view oval to rectangular, longer than wide; lateral and posterior margins slightly convex. Maxillary palps filiform, relatively short, not posteriorly surpassing beyond mid-length of head. Mandibles with masticatory margin with 1 large apical tooth, followed by 2 smaller teeth, fourth tooth larger than third, and then followed by denticles. Anterior margin of clypeus slightly emarginate medially. Scape relatively short when compared to *T. atriceps* (SI < 85), reaching or surpassing posterior margin of head by distance shorter than pedicel length. Pronotum and mesonotum form continuous feeble convexity in lateral view; metanotal groove weakly impressed; propodeum dome-shaped, slightly higher than mesonotum. Integument weakly imbricate, excepting petiole which is smooth. Body covered with short decumbent pubescence. Head (excluding clypeus), antenna, and mesosoma lacking erect setae, clypeus with 6 anterior setae. Pilosity pattern on gastric tergites similar as to *T. atriceps*. Head and gaster medium brown; antenna, mesosoma, legs, and petiole pale whitish yellow to bright orange (Fig. 1C, D). Mesosoma with brown spot on mesopleuron and lateral pronotum, sometimes present on metapleuron and lateral propodeum, almost completely covering mesosomal side.

Queen. Measurements (*n* = 6): HL 0.74 ± 0.04 (0.70–0.80), HW 0.64 ± 0.03 (0.59–0.68), SL 0.54 ± 0.04 (0.49–0.59), WL 1.24 ± 0.18 (1.07–1.46). Indices: CI 86 ± 1 (84–87), SI 73 ± 2 (70–76).

Head rectangular in full-face view, clearly longer than wide (CI 84–87); lateral and posterior margins straight. Masticatory margin of mandible with 1 large apical tooth, followed by 2 smaller teeth, fourth tooth larger than third, followed by 5 smaller teeth, and then small denticles decreasing in size. Clypeus slightly emarginate anteromedially. Scape short, never surpassing posterior margin of head (SI 72–76). Integument weakly imbricate, mesopleuron smooth. Dorsum of head with abundant, short, decumbent hairs; clypeus bearing 6 long hairs; gastric tergites with several erect setae near their posterior margins. Body medium brown; palps, flagellum, coxae, trochanters, tibiae, tarsi, and petiole whitish yellow to bright orange (Fig. 2E, F); propodeum sometimes with whitish-yellow spot on posterodorsal region. Gastric tergites I–III with pale-yellow, transverse posterior strip.

Male. Measurements (*n* = 3): HL 0.46 ± 0.02 (0.43–0.48) HW 0.46 ± 0.03 (0.43–0.48) SL 0.36 ± 0.02 (0.33–0.38) WL 0.62 ± 0.02 (0.61–0.64). Indices: CI 99 ± 2 (97–100) SI 78 ± 3 (75–82)

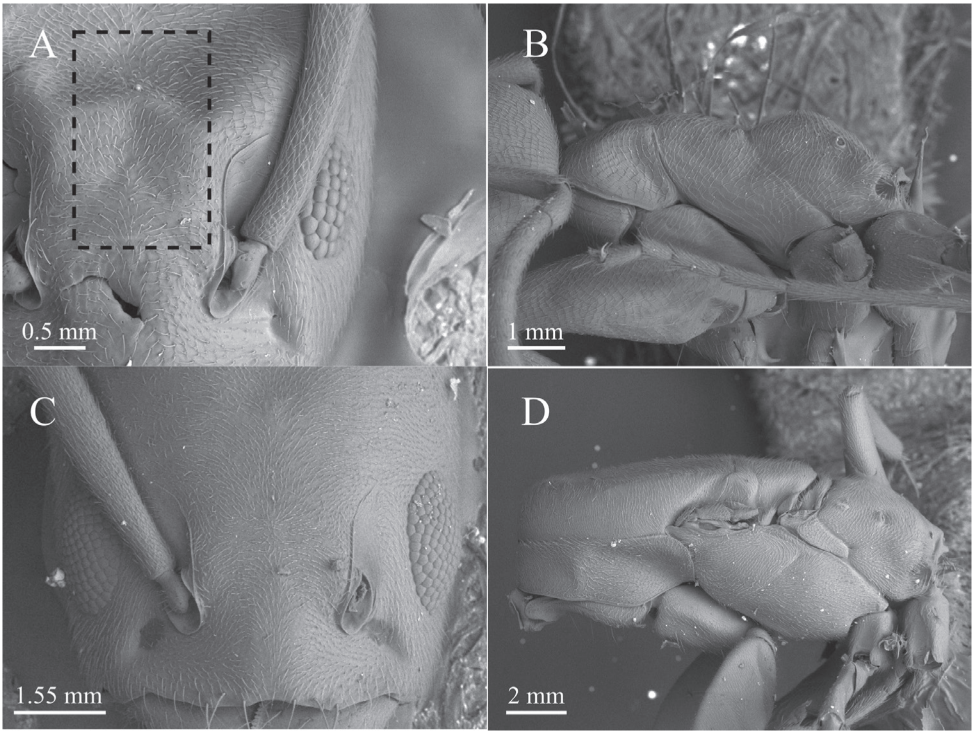

Figure 6. SEM microphotographs of *Tapinoma breviscapum* from Serra do Cipó (Minas Gerais, Brazil) **A** worker head in dorsal view **B** worker mesosoma in lateral view **C** queen head in dorsal view **D** queen mesosoma in lateral view. The inset with broken lines indicates finer and lesser separated pubescence on the frons between the frontal carinae. Specimens deposited in DZUP.

Head in dorsal view rounded, posterior margin slightly interrupted by lateral ocelli; anteromedian margin of clypeus straight to weakly emarginate. Compound eye large, rounded; scape long, reaching posterior margin of head; maxillary palp filiform. Mandible semi-falcate; masticatory margin with large apical tooth followed by many teeth of similar size. Integument feebly imbricate, katepisternum smooth. Forewing with median short; hindwing with free section of radial and cu-a present, free section of cubitus absent. Row of long setae present on posterior margins of fore and hindwing. Head, scutum, scutellum, and gaster covered by moderately abundant, yellow, short, decumbent hairs; antenna covered by short, decumbent hairs. Anepisternum covered by hairs, katepisternum lacking hairs ventrally. Gastric tergites I–V lacking erect setae. Head, mesosoma, petiole, and gaster dark brown; antenna and legs light brown.

Distribution. *Tapinoma breviscapum* has been recorded from Misiones, Argentina, and from the Brazilian states of Minas Gerais, Rio de Janeiro, and São Paulo (Fig. 5).

Biology. *Tapinoma breviscapum* is an arboreal ant, but beyond that, there is not much available information. This species, reported as *T. atriceps*, was found inhabiting a gall of *Microgramma squamulosa* (Kaulf.) de la Sota (Santos et al. 2019).

Material examined. Argentina • 3 workers; Misiones, 40.66K N Campinas de América; 25°55.153'S, 53°56.151'W; alt. 508 m; 3 Jan. 2008; W. Mackay and E. Mackay legs; WEMC#22811 BRAZIL • 2 queens, 1 worker; Minas Gerais, Alto Caparaó, Parque Nacional Caparaó; 20°25.155'S, 41°51.083'W; 5-20 Dec. 2011; J. Chaul leg.; DZUP • 2 males, 3 workers; Minas Gerais, Serra Caraça; 1380 m; Nov. 1961; K. Lenko, Martins and Silva legs; MZSP 3104 • 3 workers; Minas Gerais, Serra Caraça; 1380m; Nov. 1961; K. Lenko, Martins and Silva legs; MZSP 4216 • 1 male, 2 queens, 17 workers; Minas Gerais, Serra do Cipó, CAPIII; Jan. 2013; M. Anjos M. leg.; DZUP • 1 queen, 2 workers; Minas Gerais, Serra do Cipó, Capão 11; 19°14.873'S, 43°33.055'W; 25 Jun. 2017; H. Brant leg. DZUP • 5 workers; Minas Gerais, Serra do Cipó; 19°14.874'S, 43°33.054'W; 25 Jun. 2017; M. Escárraga leg., MYR380; Genbak codes: MG920285, MN294973, MN294963, MT375619; DZUP 548800 • 1 worker; Rio de Janeiro, Nova Friburgo, Praça do Suspiro, 22°16.763'S, 42°32.148'W; Apr. 2016-Feb. 2018; I. Lancelloti leg.; DZUP • 5 workers; São Paulo, Barueri; K. Lenko leg.; MZSP 447 • 5 workers; São Paulo, Barueri; K. Lenko leg.; MZSP 2477 • 5 workers; São Paulo, Barueri; 19 Jul. 1958; K. Lenko leg.; MZSP 534 • 3 workers; São Paulo, Cubatão, Estação Raiz da Serra; v Ihering leg.; MHNG • 2 queens, 2 workers; São Paulo, Ilha dos Búzios, 2 Apr. 1964; Exp. Dep. Zool. legs; MZSP 3910 • 1 male, 1 queen, 2 workers; São Paulo, Ilha dos Búzios, 2 Apr. 1964, Exp. Dep. Zool. legs; MZSP 4105 • 2 workers; São Paulo, Ilha dos Búzios; 3 Sep. 1964; Exp. Dep. Zool. legs; MZSP 3885 • 4 workers; São Paulo, Ilha dos Búzios; 3 Apr. 1964; Exp. Dep. Zool. legs; MZSP 3885 • 1 male, 1 queen, 3 workers; São Paulo, Ilha dos Búzios, 19 Oct. 1963; Exp. Dep. Zool. legs; MZSP 2978 • 1 queen, 4 workers; São Paulo, Ilha dos Búzios; 17 Oct. 1963; Exp. Dep. Zool. leg; MZSP 2994 • 1 queen, 4 workers; São Paulo, Ilha dos Búzios; 26 Oct. 1963; Exp. Dep. Zool. legs; MZSP 2992 • 1 queen, 3 workers; São Paulo, Ilha dos Búzios; 31 Jul. 1964; Exp. Dep. Zool. legs; MZSP 3616 • 1 male, 1 queen, 2 workers; São Paulo, Ilha dos Buzios; 2 Apr. 1964; Exp. Dep. Zool. [MZSP 4105] • 1 worker; São Paulo; MZSP11974 • 6 workers; São Paulo; USNM.

Morphological separation between *Tapinoma atriceps* and *T. breviscapum*

The most readily recognizable morphological diagnostic traits that permit separation of *T. atriceps* and *T. breviscapum* workers and queens are the relative length of the scape (i.e., SI), the shape of the propodeum, and differences in the degree of cephalic pubescence. In *T. atriceps* the worker scape is almost as long as the HL or greater (SI >93; Fig. 1A), in contrast with *T. breviscapum*, where it is relatively short (SI < 85; Fig. 1B), sometimes reaching or barely surpassing the posterior head margin by a distance shorter than the pedicel length. SL shows significant differences between the workers of each species ($T = 7.51$, $p < 0.0001$). Although there is a certain degree of overlap in the absolute measure (0.50–0.63 in *T. atriceps* and 0.44–0.56 in *T. breviscapum*) the relationship from SL to HL for each species showed non-overlapping ranges (Fig. 7). Other morphometric traits, such as HL, HW, and WL were also evaluated; however, each of their paired distributions overlapped, showing no statistical differences. The

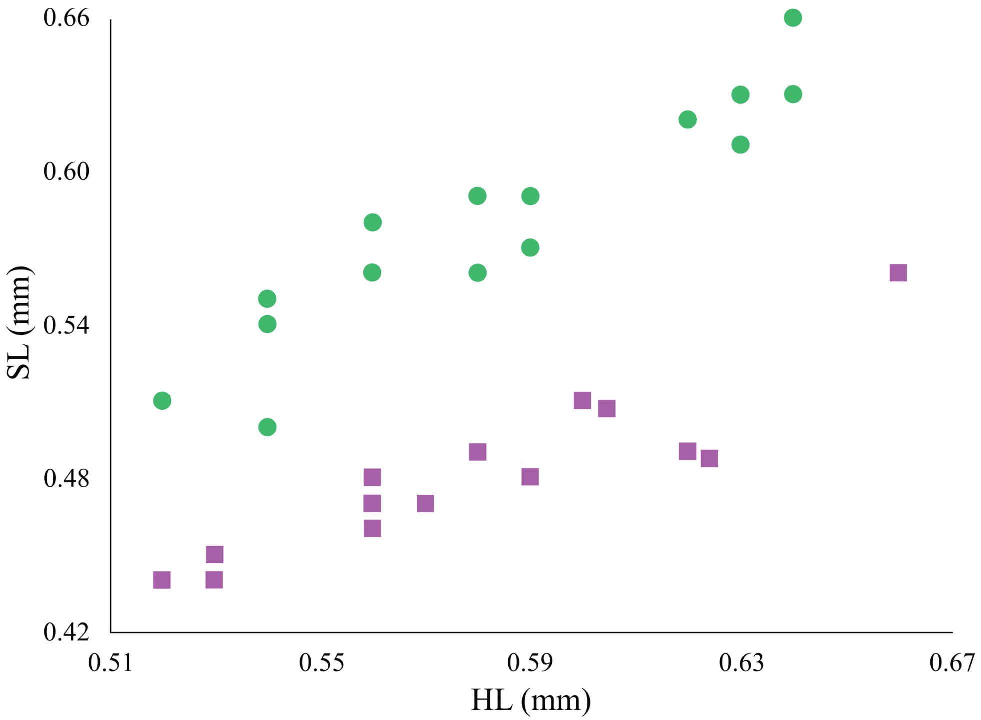

Figure 7. Morphometric scatterplot showing the relationship between HL and SL. The green circles correspond to the measurements of *Tapinoma atriceps*, while the purple squares correspond to those in *T. breviscapum*.

SL partially overlaps in queens of both species (0.58–0.62 in *T. atriceps* and 0.49–0.59 in *T. breviscapum*); however, differences between species were found ($T = 2.29$, $p = 0.0257$). These differences are notable in the non-overlapping ranges of the relative length of the scape (82–83 and 70–76, respectively). Statistical differences were also found in the HW of both species ($T = 2.26$, $p = 0.0268$); even without measuring, these differences are evident when they are compared under a stereoscope (Fig. 2B vs 2E), as *T. breviscapum* queens have a more elongate head as reflected in CI values that do not overlap those of *T. atriceps* queens.

The worker propodeum in both species differs markedly in shape and in the proportions between the dorsal and the posterior faces (Fig. 4B vs 6B). The dorsal propodeal margin when seen laterally in *T. atriceps* forms a distinct blunt angle with the declivity, contrasting with the rounded convexity formed in *T. breviscapum*. Additionally, the dorsal margin in *T. atriceps* is about 1/4 the length of the declivitous margin, while in *T. breviscapum* it is longer, about 1/2 that of the declivity (Figs 1B, D, 4B, 6B). The dorsal surface of the head in *T. atriceps* workers (Fig. 4A) is covered by appressed pubescence that is relatively longer and sparser than in *T. breviscapum*, where it is abundant and relatively shorter (Fig. 6A). The males of both species are relatively similar in morphology(Fig. 3), but the male of *T. breviscapum* can be differentiated from

T. atriceps males because the former is on average slightly larger (0.63 ± 0.02 mm) and the scutellum is glabrous, while males of *T. breviscapum* are slightly smaller (0.62 ± 0.02 mm) and have decumbent hairs on the scutellum.

Genetic differentiation between *Tapinoma atriceps* and *T. breviscapum*

Final alignments had 648, 562, 422, and 655 bp for COI, LW Rh, Wg, and EPIC, respectively. For LW Rh, the length of the concatenated two flanking exonic sequences was 456 bp and for the intron 106 bp.

The greatest genetic variation among the molecular markers was observed in COI, followed by EPIC, Wg, LW Rh-ex, and LW Rh-in, with 114, 38, 15, 9, and 3 variable sites, respectively. Within the *T. atriceps* samples, the genetic pairwise distance ranged between 0.0–9.6% for COI, 0.0–2.0% for LW Rh-intron and Wg, 0.0–1.8% for EPIC, and 0.0–0.4% for LW Rh-exon. The mean genetic distance between *T. atriceps* and *T. breviscapum* was 9.4% (8.8–10%) for COI. For the nuclear markers, EPIC presented the greatest distance between the two species (4.6–4.7%), followed by Wg (1.4–5.9%), LW Rh-intron (1.1–2.3%), and LWRh-exon (1.5–1.7%).

In the phylogenetic reconstruction (Fig. 8A), *T. opacum* is closer to *T. atriceps* and *T. breviscapum* than to *T. melanocephalum*. *Tapinoma atriceps* was recovered as a monophyletic group, sister to *T. breviscapum*. The Bayesian consensus trees of the individual analysis of each locus also recover both results (Suppl. material 4: Figure S1). Bayesian analysis of COI provided a topology similar to the Bayesian tree based on concatenated data, although with differences in branch lengths and node support of *T. atriceps* (PP = 0.71). The reconstructed separate trees with the nuclear loci also recovered *T. breviscapum* as a sister species to *T. atriceps* (Suppl. material 4: Figure S1) but the latter results in poor resolution among the sampled populations. Within *T. atriceps*, the topology derived from the concatenated data was relatively similar to the haplotype network (Fig. 8B). The samples from Paraná, corresponding to haplotypes H05 and H06, presented a comparatively deep divergence from the rest of the species. The sample of *T. atriceps* from Minas Gerais was sister to the group from southern Brazil, the populations of this latter group showing little genetic structure. Most of the nodes were relatively well-supported (PP 0.85–1.00) except for the low value of support corresponding to the Antonina haplotype (H01).

Seven mitochondrial (COI) haplotypes of *Tapinoma atriceps* were identified for the eight analyzed sequences and a single mitochondrial haplotype for the only *T. breviscapum* sample (Fig. 8B). The analysis estimated five unsampled haplotypes and found many mismatches between most of the haplotypes, evidencing high molecular variation for this marker. Haplotype H01, found in Paraná and Santa Catarina, is very close to haplotypes H02 and H03 and separated from them by only one nucleotide substitution; together, these form a group of haplotypes from southern Brazil. Other two haplotypes found in Paraná (H05 and H06) are relatively close to each other, and separated by one unsampled haplotype, but very different from the other haplotypes from Paraná. Haplotype H04 from Minas Gerais is closest to the H01–H03 haplotype group, separated by two unsam-

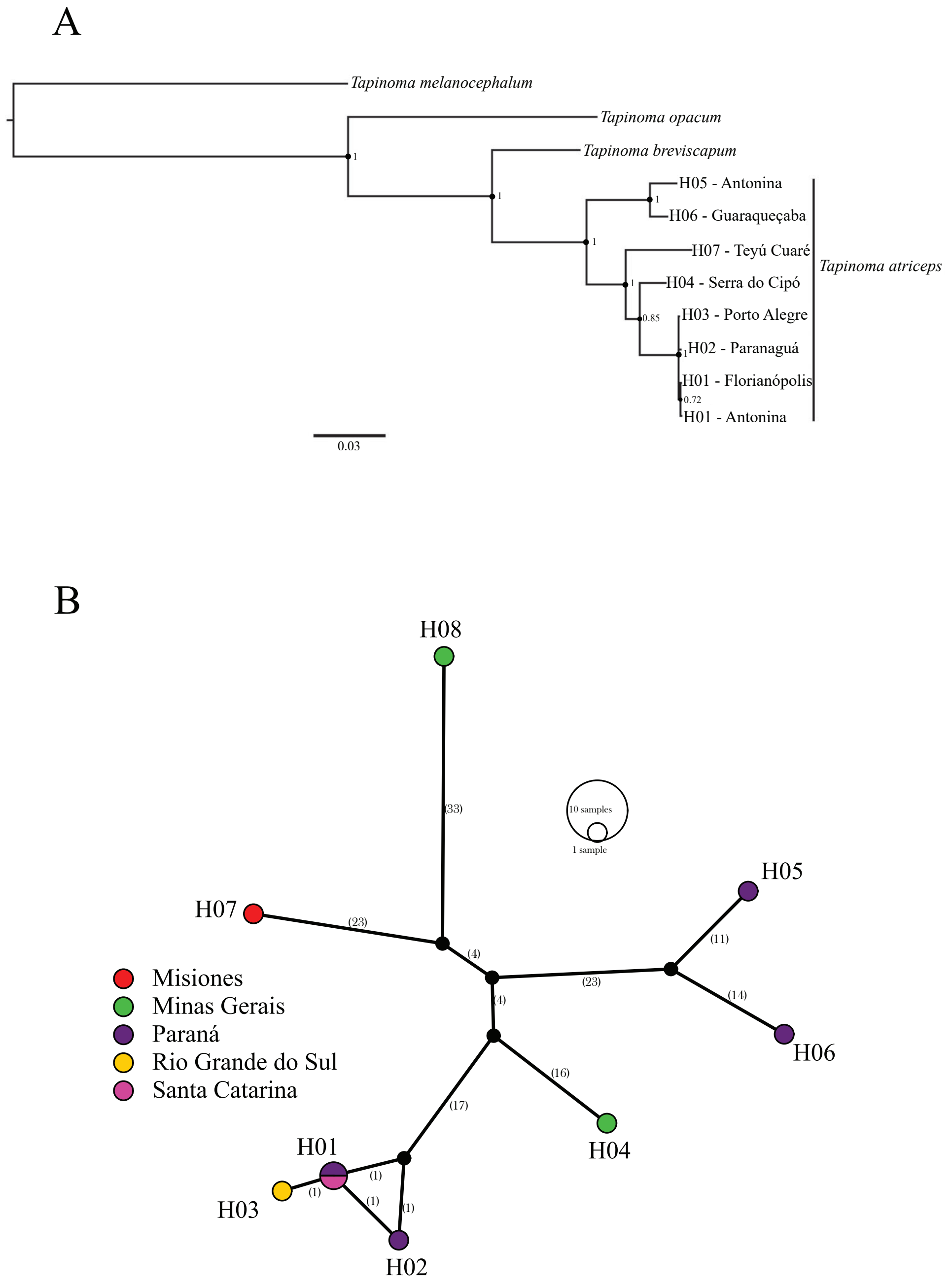

Figure 8. Evolutionary relationships between *Tapinoma atriceps* and *Tapinoma breviscapum* **A** bayesian phylogenetic reconstruction based on concatenated sequences of four molecular markers (COI, LWRh, WG, and EPIC). The scale bar represents substitutions per site and the number next to nodes the posterior probability **B** haplotype network including several populations of *T. atriceps* and a single sample of *T. breviscapum* (H08). Every circle represents a different haplotype, the color corresponds to the geographical distribution, and the number between brackets corresponds to the number of mismatches between haplotypes.

pled haplotypes. Haplotype H07 from Misiones (Argentina) is closer to *T. breviscapum* haplotype (H08) and relatively close to the subset of haplotypes from the southeastern (H04) and southern Brazil (H01–H03). A haplotype network built with only the sampled populations of *T. atriceps* (Suppl. material 5: Figure S2) shows that the H07 haplotype is sister to the other haplotypes from southeastern and southern Brazil, which is congruent with the phylogenetic structure inferred from the concatenated molecular data (Fig. 8A).

Discussion

Tapinoma atriceps and *Tapinoma breviscapum* can be differentiated from other Neotropical *Tapinoma* ants by their particular bicolored pattern. Other *Tapinoma* can be mostly pale yellow or uniform brown, with yellow antennal scapes and coxae, but never with a spot on the mesopleuron, nor the bicolored pattern of *T. atriceps* and *T. breviscapum*. Only two other ant species that occur in South America, *Tapinoma melanocephalum* (Fabricius, 1793) and *Linepithema leucomelas* (Emery, 1894), have similar colors and size that could lead to confusion. In the case of *T. melanocephalum*, a common invasive species, the head and mesosoma is dark brown and the gaster is pale yellow (Guerrero 2018). *Linepithema leucomelas* can be differentiated by the characters that define the genus: presence of a well-developed petiolar scale and mandibular dentition which presents teeth alternating with denticles (Wild 2007b).

Tapinoma atriceps and *T. breviscapum* are typical representatives of the genus in the Atlantic Forest of southwestern Brazil. Because of their sympatric distribution and morphological similarity, it has been difficult to separate them and the name *T. atriceps* has prevailed. Before the present work, *T. breviscapum* was only known from the type locality, Raiz da Serra in São Paulo (Forel 1908). We found that this species has a broader distribution, occurring in other Brazilian states such as Minas Gerais and Rio de Janeiro, and as far south as Misiones, Argentina. Such a broad distribution raises questions about the geographical origin of both species, which must be analyzed through a robust phylogeny and biogeographic inference of the genus *Tapinoma* in the Neotropical region.

Morphologically, *T. atriceps* and *T. breviscapum* can be differentiated by metric features associated with the head of the worker and queen, while the shape of the propodeum and hairs on the head allows the separation between the workers of both species, but the color of the body of the workers and queens in both species is relatively similar (see taxonomic treatment). Although the latter is true when species are allopatrically distributed, when occurring sympatrically they may exhibit no overlap of this trait (i.e., perhaps evidencing character displacement). The coloration pattern of workers and queens of *T. atriceps* and *T. breviscapum* from Serra do Cipó (MG, Brazil), corresponding to haplotypes H04 and H08, respectively, contrasts notably: antenna, mesosoma, legs, and petiole pale whitish-yellow in *T. atriceps* (Figs 1A, B, 2A, B) while those same sclerites are bright orange in *T. breviscapum* (Figs 1C, D, 2E, F). Differences in color are also observed in the worker and queen of both species from Misiones (Argentina), but the same sclerites which are bright orange in *T. breviscapum* are paler when compared to the H08 haplotype (R. Guerrero personal observation). This contrasting coloration pattern in sympatry could have played a fundamental role in the separation of lineages by reinforcing reproductive barriers between *T. atriceps* and *T. breviscapum* populations. The integration of comparative morphological analyzes of the genitalia of the males in both species and the analysis of more molecular data are necessary to elucidate aspects related to this evolutionary hypothesis.

The molecular analyses, including both mitochondrial and nuclear data, support the monophyly of *T. atriceps* (Fig. 8A), but we could not assess the monophyly of *T. breviscapum* because we could only analyze one sample of this species. The preliminary phylogenetic results of a broader study of *Tapinoma*, which includes several samples of both species from Minas Gerais and Misiones, confirm the reciprocal monophyly between them (R.J. Guerrero unpublished data). The COI-based Bayesian tree (Suppl. material 4: Figure S1) and the mitochondrial haplotype network (Fig. 8B) are very similar to the concatenated Bayesian tree, showing only minor differences in the position of the Misiones haplotype (H07) within *T. atriceps*. The other molecular markers also recovered *T. breviscapum* as sister to *T. atriceps* but failed to establish relationships among *T. atriceps* populations. Congruence between COI and the other nuclear markers is likely to be the result of similar differential lineage sorting. Although the Bayesian trees of COI and EPIC (Suppl. material 4: Figure S1) result in topologies with consistently different branch lengths, both markers show a similar phylogenetic relationship pattern within *T. atriceps*.

The average genetic distance between *T. breviscapum* and *T. atriceps* using COI (9.4%) is relatively high when compared with other *Tapinoma* species. For instance, Seifert et al. (2017) found genetic distances varying between 1.8% and 4.8% for pairs of *Tapinoma* species from the Mediterranean region using the same marker, considerably smaller values than those found in this study. The intraspecific variation in COI for *T. atriceps* is also considerably high (maximum of 9.6%) in comparison with *T. ibericum* Santschi, which has a distance of 1.3% as the greatest intraspecific variation (Seifert et al. 2017).

The highest values of intraspecific genetic distance in *Tapinoma atriceps* (9.6%) overlap with those between *T. breviscapum* and *T. atriceps* (8.8–10%); however, the greatest variation within *T. atriceps* species was found by comparing two samples from Paraná (H05–H06) with the rest of *T. atriceps* populations (Fig. 8B, Suppl. material 5: Figure S2). Such high genetic distance suggests the existence of cryptic diversity within this taxon, perhaps as the result of past climatic changes in the southern Atlantic Forest (Ströher et al. 2019), but divergence times estimates are necessary to obtain an approximation to this remarkable intrapopulation genetic differentiation. Despite the cryptic diversity suggested by COI we did not find any distinct morphological character in the workers and queens from Paraná (H05–H06) that would allow them to be separated from other *T. atriceps* specimens; therefore, we suggest these populations as part of the metapopulation of *T. atriceps* distributed in the Brazilian Atlantic Forest. Morphological analysis of more specimens, mainly males, in a wider geographical sampling throughout the Atlantic Forest biome could shed light on the intrapopulation mitochondrial genetic variation found in *T. atriceps*.

Conclusions

We found that a native *Tapinoma* occurring in the Atlantic Forest and previously considered as different phenotypes of the same species, correspond in fact to two different species, *Tapinoma atriceps* and *Tapinoma breviscapum*, based on morphological and molecular evidence. We also found high COI variation within *T. atriceps* populations, suggestive of cryptic diversity. However, these results should continue to be explored with a broader sampling, as more population samples might be needed to understand phylogeographic patterns in *T. atriceps* and *T. breviscapum*. Additionally, those phylogeographic patterns could help in understanding the biogeographic history of the Atlantic Forest. Finally, a complete phylogenetic framework is needed to understand the origin and evolution of *Tapinoma* in the Neotropical region.

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Supplementary material 1

Table S1. Results of Normality test of the data in workers, queens, and males of *Tapinoma atriceps* and *T. breviscapum*

Authors: Mayron E. Escárraga, John E. Lattke, Marcio R. Pie, Roberto J. Guerrero

Data type: statistical data

Explanation note: *n* = number of specimens included in the analysis. SD = Standard deviation. W= Shapiro–Wilk test. *p* = probability associated with the distribution of the statistical test W. * indicates those morphometric characters that showed normality.

Link: https://doi.org/10.3897/zookeys.1033.59880.suppl1

Supplementary material 2

Table S2. Genbank codes of DNA sequences of *Tapinoma melanocephalum* and *T. opacum*, downloaded from Genbank

Authors: Mayron E. Escárraga, John E. Lattke, Marcio R. Pie, Roberto J. Guerrero

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.1033.59880.suppl2

Supplementary material 3

Table S3. Substitution models selected with PartitionFinder v. 2.1 for each genetic marker

Authors: Mayron E. Escárraga, John E. Lattke, Marcio R. Pie, Roberto J. Guerrero

Data type: molecular data

Link: https://doi.org/10.3897/zookeys.1033.59880.suppl3

Supplementary material 4

Figure S1. Bayesian consensus trees from analyses of individual loci.

Authors: Mayron E. Escárraga, John E. Lattke, Marcio R. Pie, Roberto J. Guerrero

Data type: phylogenetic tree

Explanation note: Nodes with posterior probabilities greater than 80% are marked with circles. Posterior probabilities less than 80% are included. The scale bar represents substitutions per site and the number next to nodes the posterior probability. Outgroups have been pruned.

Link: https://doi.org/10.3897/zookeys.1033.59880.suppl4

Supplementary material 5

Figure S2. Haplotype network including only *T. atriceps* populations

Authors: Mayron E. Escárraga, John E. Lattke, Marcio R. Pie, Roberto J. Guerrero

Data type: occurrence

Explanation note: The haplotype numbers are the same as in Table 1 and Figure 8B. Every circle represents a different haplotype, the color corresponds to the geographical distribution, and the number between brackets corresponds to the number of mismatches between haplotypes. Acronyms correspond to the states in Brazil, namely: MG, Minas Gerais; PR, Paraná, RS, Rio Grande do Sul; and SC, Santa Catarina.

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RESEARCH ARTICLE

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Genome sequencing reveals extraordinary cephalic horns in the Madagascan dung beetle genus *Helictopleurus* (Coleoptera, Scarabaeinae): insight from a revision of *fungicola* species group

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Abstract

In this study, we test and corroborate the phylogenetic position of *Heterosyphus* within *Helictopleurus* using mitogenomes and nuclear loci. Our recent samplings revealed that males of the former *Heterosyphus sicardi* Paulian, 1975 (today under *Helictopleurus* d'Orbigny, 1915) have extraordinary bilateral clypeal horns which are exclusive within the genus. We provide a taxonomic review of the *fungicola* species group of *Helictopleurus* and discuss the systematic position of *H. sicardi* within the group. The male phenotype of *H. sicardi* is described and photographs of the body and genitalia of the members of the *fungicola* group are given, as well as a diagnostic key to species of the group. *Helictopleurus fungicola peyrierasi* is considered to be a distinct species within the genus (*H. peyrierasi* **stat. rest.**). *Helictopleurus pluristriatus* d'Orbigny, 1915 **syn. nov.** is established as a junior synonym of *H. fungicola* (Fairmaire, 1899).

Keywords

dung beetles, *fungicola* species group, *Heterosyphus*, Madagascar, male horns, mitogenomics, Scarabaeinae

Introduction

The dung beetle tribe Oniticellini (Coleoptera, Scarabaeinae) was represented by two endemic genera in Madagascar, namely *Helictopleurus* d'Orbigny, 1915 and *Heterosyphus* Paulian, 1975. With 68 known species and subspecies, *Helictopleurus* was thought to have males with only simple cylindrical horns or carina on the head, which are common across various dung beetle lineages. At the same time, the monotypic and extremely rare *Heterosyphus* was thought to be hornless. Previous phylogenetic analysis of Madagascan Oniticellini (Wirta et al. 2008) revealed a nested position of *Heterosyphus* within *Helictopleurus*; following these results Philips (2016) suggested the synonymy of *Heterosyphus* with *Helictopleurus*.

Helictopleurus sicardi, the former member of the monotypic genus *Heterosyphus* (Paulian 1975), has been known so far by only four females and one hornless male from the northern Madagascar (Montagne d'Ambre) (see Material examined). Recent sampling of forest leaf litter yielded new specimens of this rare species, whose biology is still enigmatic. Two of those specimens are males with two spectacularly long horns that arise from the lateral sides of the clypeus. This polymorphism in males – presence vs. absence of horns – is common among dung beetles. Nonetheless, the bilateral clypeal horns observed in *H. sicardi* are unique within *Helictopleurus* and rare in other genera of the tribe Oniticellini and its sister, the tribe Onthophagini. It is noteworthy that similar bilateral clypeal horns occur in more distant dung beetle lineages such as, for example, the genera *Heliocopris* Hope, 1837 and *Bubas* Mulsant, 1842.

Thus, considering the exclusive phenotype of *H. sicardi* and its previous placement in a separate genus, we test the phylogenetic position of this species within *Helictopleurus* using mitogenomic data and nuclear loci. Our 19-gene phylogenetic analysis of *Helictopleurus* and other genera from the tribe Oniticellini corroborates the results of Wirta et al. (2008) by supporting the synonymy of *Heterosyphus* with *Helictopleurus*. Both morphological and molecular evidence suggest that *H. sicardi* is a member of the *fungicola* species group (*sensu* Montreuil 2005a) of *Helictopleurus*. We describe the male phenotype of *H. sicardi*, discuss the taxonomy and systematic position of the *fungicola* species group, reconsidering the status of *H. fungicola peyrierasi* and proposing *H. pluristriatus* as a junior synonym of *H. fungicola*.

Material and methods

Material deposition

Voucher specimens and type material analyzed throughout the study are deposited in the following institutes:

MNHN	Muséum national d'Histoire naturelle, Paris;
MZHF	Finnish Zoology Museum of Natural History (LUOMUS), Helsinki (S. Tarasov, J. Mattila).

Morphological examination

The external morphology, along with the anatomy of the male and female genitalia of a total of 39 *Helictopleurus* species currently assigned to seven of the nine species groups (Lebis 1960; Montreuil 2005a) were examined. The identification of the specimens was carried out by comparison with the name-bearing type material. Following the methodology of Tarasov and Génier (2015), at least one male and one female per species were completely disarticulated for a comprehensive scrutiny of their morpho-anatomy. Body parts were subsequently washed with distilled water and stored on tissue culture plates with glycerol. Male and female genitalia were cleaned in the KOH solution before being stored in glycerol, while hindwings were placed in glycerol after dissection.

Morphological study was performed under a Leica S9D stereomicroscope. Habitus photographs were taken with a Canon EOS 5D camera and a Canon MP-E 65mm, f/2.8, 1–5× macro lens, using the Cognisys Stackshot automated system; male genitalia were photographed with a Nikon SMZ25 stereomicroscope coupled with a DS-Ri2 camera. Zerene Stacker (v. 1.04 Build T2020-05-22-1330) software and NIS-Elements-BR (Nikon Imaging Software Basic Research) were used to process and combine multiple photographs. Images were enhanced and arranged in plates in Adobe Photoshop and Illustrator CC 2015.

Molecular dataset

DNA extraction, library preparation and sequencing

Genomic DNA was extracted from an ethanol-preserved female of *H. sicardi* (http://id.luomus.fi/NC.03) following the Qiagen DNeasy Blood & Tissue Kit (QIAGEN). The quality control was performed with a Qubit dsDNA HS (Invitrogen) and Fragment Analyzer (AATI). The generated Nextera Flex library (Illumina) was sequenced using Illumina NextSeq 500 sequencer with the cycles 170-8-8-132 that yielded the lowest coverage genome of *H. sicardi*.

Genome assembly and annotation

The read quality was checked with FastQC (Andrews 2010) and adapters were removed using Trimmomatic (Bolger et al. 2014). The trimmed reads were mapped against the reference mitogenome of *H. quadripunctatus* (accession number KU739489) using BWA software and its bwa-mem algorithm (Li and Durbin 2009). This allowed us to assemble ~85% of *H. sicardi* mitogenome (accession number: MW759025) used in the downstream analyses. The assembled mitogenome was annotated in Geneious using the reference mitogenome of *H. quadripunctatus* (Olivier, 1789).

Molecular dataset

The ingroup consisted of 44 operational taxonomic units (OTUs) belonging to ~30 species of *Helictopleurus*; two *H. sicardi* OTUs were used, the new one and the one from previous phylogenetic study (Wirta et al., 2008). The outgroup included nine species from various Afrotropical and Oriental lineages of Oniticellini. The dataset comprised 13 protein-coding and two rRNA genes (16S and 12S) from mitogenome, and two nuclear rRNA genes (18S and 28S). Thus, our molecular dataset included novel sequences for *H. sicardi*, as well as GenBank data for *Helictopleurus* and Oniticellini from mitogenomic (Breeschoten et al. 2016) and individual genes (Wirta et al. 2008; Monaghan et al. 2009; see Suppl. material 1) phylogenetic studies. The dataset was compiled using phylotaR (Bennett et al. 2018) and AnnotationBustR (Borstein and O'Meara 2018).

Phylogenetic analyses

Gene fragments were individually aligned using MAFFT (Katoh et al. 2002) and concatenated into five prior partitions: three codon partitions, mitochondrial rRNA and nuclear rRNA. The best partitioning scheme and substitution model was selected using ModelFinder (Lanfear et al. 2012) implemented in IQ-TREE (Nguyen et al. 2015) under Bayesian Information Criterion; the best-found scheme matched the prior one. The ModelFinder results were used in the subsequent IQ-TREE search to infer the maximum likelihood (ML) tree. The support values (i.e., bootstrap support, BS) were calculated using ultrafast bootstrap approximation (Minh et al. 2013).

Results and discussion

Phylogenetic analyses

The combined phylogenetic analyses of the fragments of 19 mitochondrial and nuclear genes support the monophyly of the genus *Helictopleurus* (BS 83) (Fig. 1A). The recovered relationships among Oniticellini genera are consistent with the mitogenomic study of Breeschoten et al. (2016). *Helictopleurus sicardi* (both OTUs used) is nested within *Helictopleurus* as the sister species to *H. fungicola* (BS 100). These findings are also supported by the earlier 5-gene phylogenetic analysis of *Helictopleurus* (Wirta et al. 2008). The clade *sicardi+fungicola* and its sister (BS 87) together form sister to the *semivirens* clade and define the first divergence event within the genus.

Interestingly, our combined analysis and that of Wirta et al. (2008) place another member of *fungicola* species group, *H. peyrierasi* stat. rest. (see discussion below), as sister of the *viridiflavus* clade (BS 77, Fig. 1A). However, morphological synapomorphies (see below) and a separate analysis using only COI support the position of *H. peyrierasi* as the sister to *sicardi+fungicola* clade (BS 80) (Fig. 1B). In our and Wirta et al.'s (2008) analyses, only three gene fragments (COI, 28S, 16S) were available for *H. peyrierasi*. We believe that the placement of *H. peyrierasi* as sister of the clade *viridiflavus* is an artefact of the data deficiency. Following the morphological evidence and COI results, we continue to treat *H. peyrierasi* as a member of the *fungicola* group, while *H. neoamplicollis* is excluded from it.

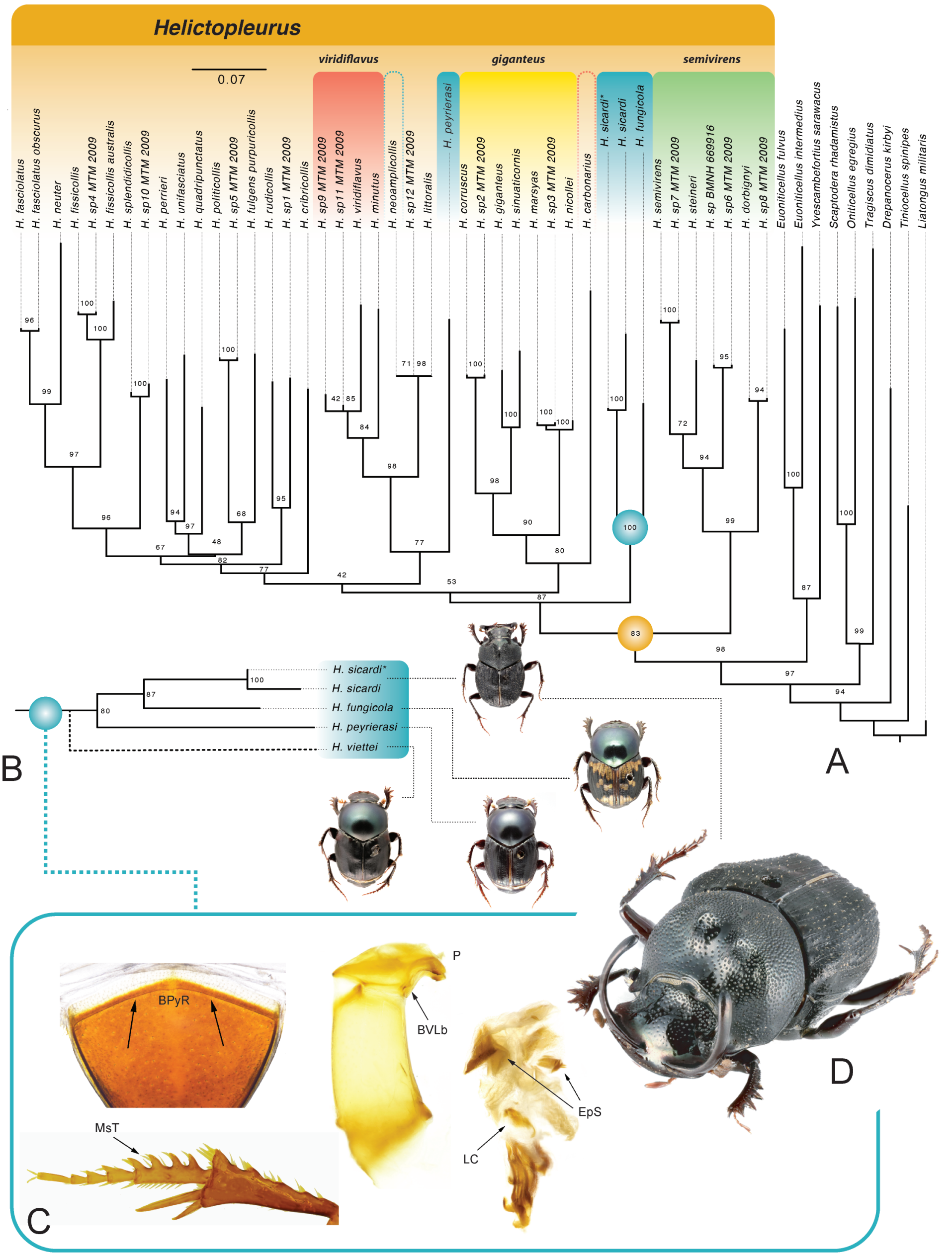

Figure 1. Molecular phylogenies and morphological synapomorphies of the *fungicola* species group **A** phylogenetic position of *H. sicardi* within *Helictopleurus*. *Helictopleurus neoamplicollis* and *H. carbonarius* are highlighted with colored dashed line to indicate their previous placement **B** COI-based phylogeny: magnification of the *fungicola* clade and phylogenetic position of *H. peyrierasi* stat. rest. **C** synapomorphies of the *fungicola* species group: basal pygidial ridge (BPyR); mesotarsal teeth (MsT) on the first tarsomere; parameres (P) elongated and evenly curved downward, basoventral lobes of the parameres bell shaped (BVLb); superior side of the membranous sac of the endophallus with spines (EpS); lamella copulatrix very simple (LC) **D** detail of the clypeal horns of the male of *H. sicardi*.

Systematics and diagnosis of the *fungicola* species group

According to Montreuil (2005a), the *fungicola* group includes the following six species: *H. fungicola*, *H. peyrierasi* stat. rest. (see discussion below), *H. viettei* Paulian & Cambefort, 1984, *H. pluristriatus* d'Orbigny, 1915, *H. neoamplicollis* Krell, 2000, and *H. nigritulus* Lebis, 1960. Here we examined the morphology of 39 *Helictopleurus* species belonging to all the currently known species groups (*sensu* Montreuil 2005a) to elucidate putative synapomorphies and formulate a new definition of the *fungicola* clade recovered in our molecular analyses. The morphological study suggests that the *fungicola* group consists of four species: *H. sicardi*, *H. fungicola*, *H. peyrierasi*, and *H. viettei*. The monophyly of the group is supported by the following putative synapomorphies that can be equally used as diagnostic characters to define the same group (Fig. 1C): abdominal tergites 7th and 8th separated by a thin and distinct ridge; proximal mesotarsomere with spine-like spurs on the lateral edge; parameres elongated and evenly curved downward at the apex; tip of the parameres outwardly oriented; superior region of the membranous endophallus (internal sac) with elongated or scale-like, symmetrically or non-symmetrically distributed spines; and lamella copulatrix simple if compared to the remaining *Helictopleurus* species and composed of one to two close parts connected by a thin and weakly sclerotized region. *Helictopleurus viettei* is the only species of the *fungicola* group not represented in our molecular analyses, but the external and genital morphology of this species suggests its incorporation in the same group (Fig. 1B).

These putative synapomorphies are not found in *H. nigritulus* or in *H. neoamplicollis*, which were formerly assigned to the *fungicola* group. *Helictopleurus nigritulus* exhibits characters that suggest its membership in the *semivirens* group (e.g., pronotum clearly larger than elytral width, surface of the body polished, with very shallow punctures, and head of the female ogive-shaped, with a transverse and straight carina in the frontoclypeal region). The correct taxonomic placement of *H. neoamplicollis* needs further investigation. *Helictopleurus pluristriatus* is here considered to be a new synonym of *H. fungicola* (see below).

Interestingly, *H. villiersi* Paulian & Cambefort, 1984, which was assigned to the *viridiflavus* group (Montreuil 2005a), has the lateral edge of the proximal mesotarsomere serrate as in the species of the *fungicola* group. However, the phylogenetic position of *H. villiersi* remains uncertain.

Key to the species of the fungicola group

1 Pronotal punctation strong and coarse; elytral interstriae granulose; major male with long and widely curved clypeal horns (Fig. 4A–C) .... ***H. sicardi* (Paulian, 1975)**

– Pronotal punctation very fine; elytral interstriae without granules; male without horns **2**

2 Clypeal margin of male and female with two acute teeth at middle; male with a small transversal clypeal carina (Fig. 3A, B) .... ***H. viettei* Paulian & Cambefort, 1984**

– Clypeal margin of male and female with three blunt to acute teeth at middle; male without clypeal carina...**3**

3 Frontoclypeal region with a distinct hump, postoccipital margin with a pointed tubercle in the middle (Fig. 2P); external tip of the parameres without a small indentation; basoventral lobes of the parameres big and wide (Fig. 2H, I); superior side of the membranous sac of the endophallus with small to medium-sized, scale-like spines (Fig. 2M, N); lamella copulatrix consisting of two leaf-like parts (Fig. 2J) ....***H. peyrierasi* Paulian & Cambefort, 1984 stat. rest.**

– Frontoclypeal region and postoccipital margin simple to slightly swollen (Fig. 2O); external tip of the parameres with a small indentation; basoventral lobes of the parameres small and narrow (Fig. 2C, D); two patches of the superior side of the membranous sac of the endophallus are covered by long, thick and uprightly oriented spines (Fig. 2K, L); lamella copulatrix consisting of a single leaf-like parts (Fig. 2E) .... ***H. fungicola* (Fairmaire, 1899)**

***Helictopleurus fungicola* (Fairmaire, 1899)**

Figure 2A–E, K, L, O

Oniticellus fungicola Fairmaire, 1899: 519.

Helictopleurus fungicola: d'Orbigny, 1915: 425; Boucomont and Gillet 1927: 110; Lebis 1960: 97; Paulian 1986: 105; Paulian and Cambefort 1991: 115; Montreuil 2005a: 133; Orsini et al. 2007: 157 (appendix 1); Wirta et al. 2008: 1081 (phylogeny), 1085 (appendix A).

Helictopleurus pluristriatus d'Orbigny, 1915: 426 (syn. nov.); Boucomont and Gillet 1927: 111; Lebis 1960: 102; Paulian 1986: 106; Montreuil 2005a: 133.

Type material examined. Of *H. fungicola*: lectotype, male (here designated): "Madag^{r} Suberb^{lle} H. Perrier / Muséum Paris Madagascar Perrier de la Bathie Coll. L. Fairmaire 1906 / TYPE / Oniticellus fungicola Frm Madag / Oniticellus fungicola Fairmaire, 1899 Rossini et al. des. 2021 / LECTOTYPE / Helictopleurus fungicola (Fairmaire, 1899) Rossini et al. det. 2021" (MNHN).

Of *H. pluristriatus*: holotype, male: "Muséum Paris Madagascar Expéd. La Bonite, Gaudichaud 1837 / pluristriatus n. sp. d'Orb. / HOLOTYPE" (MNHN).

Distribution. This species is distributed from the northernmost region of Madagascar to the central-western coast. It is known from the Diana, Melaky, Boeny, and Menabe regions.

Remarks. The examination of the holotype of *H. pluristriatus* (Fig. 3F, G) revealed that d'Orbigny (1915) described this new *Helictopleurus* using a male of *H. fungicola*

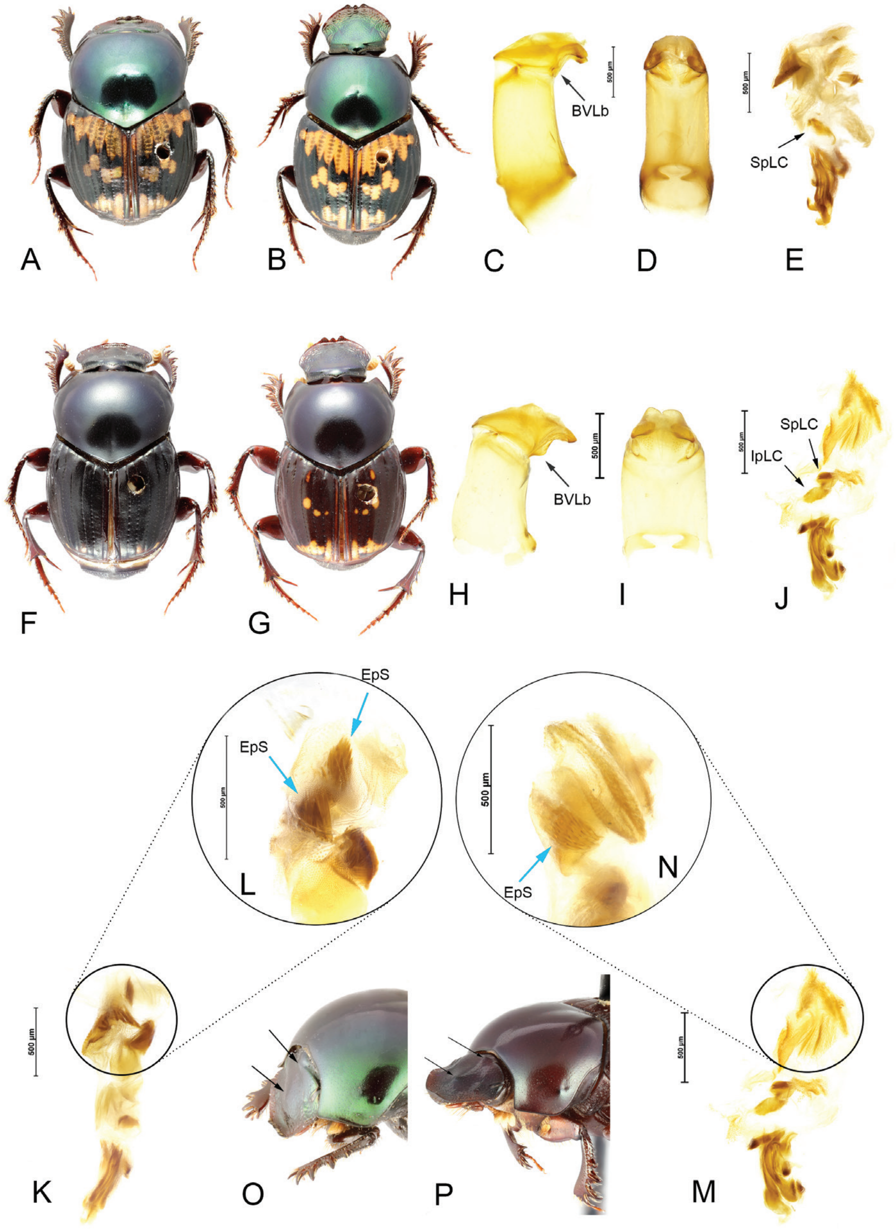

Figure 2. *Helictopleurus fungicola* **A, B** habitus of male (**A**) and female (**B**) **C, D** lateral and anterior view of the aedeagus; basoventral lobes (BVLb) **E** endophallus: lamella copulatrix (LC) **K, L** details of the superior side of the membranous sac of the endophallus; Endophallic spines (EpS) **O** lateral view of the head: arrows indicating the absence of humps and tubercles. *Helictopleurus peyrierasi* stat. rest. **F, G** habitus of male (**F**) and female (**G**) **H, I** lateral and anterior view of the aedeagus **J** endophallus: superior (SpLC) and inferior (IpLC) part of the lamella copulatrix **M, N** details of the superior side of the membranous sac of the endophallus **P** lateral view of the head: arrows indicate the frontoclypeal hump and the postoccipital central tubercle.

with no exact collecting locality. Hence, *H. pluristriatus* syn. nov. is here treated as junior synonym of *H fungicola* (Fig. 3F, G). *Helictopleurus pluristriatus* was described from a singleton male specimen allegedly collected in Madagascar (locality unknown) by the French botanist C. Gaudichaud-Beaupré during his expedition on board *La Bonite*. All observations, including all the zoological and botanical specimens collected during the expedition were later reported in the *Voyage autour du monde exécuté pendant les années 1836–1837 sur la corvette "La Bonite*", which was published in 15 volumes (Vaillant 1840–1866; Bousquet 2016). The only stop made by *La Bonite* in the Malagasy region was at Mascarene island, La Réunion. From there the frigate sailed straight toward the Cape of Good Hope (South Africa). Therefore, Gaudichaud could have received the holotype of *H. pluristriatus* from other Madagascar collectors, such as A. Pervillé and J.M.C. Richards with whom he had frequently corresponded and exchanged botanical material. Indeed, nowadays, many of Gaudichaud specimens from Madagascar are thought to have been donated to him by these two French botanists, who were the earliest to have collected natural history specimens in Madagascar. At the moment, we can rule out the possibility that the holotype of *H. pluristriatus* has been collected in La Réunion, as no *Helictopleurus* are today recorded from the island, but just a few introduced *Onthophagus* species (Lacroix and Poussereau 2019). However, its exact collecting locality in Madagascar remains unknown.

Helictopleurus peyrierasi Paulian & Cambefort, 1991 stat. rest.

Figure 2F–J, M, N, P

Helictopleurus peyrierasi Paulian & Cambefort 1991: 115; Montreuil 2005a: 133.
Helictopleurus fungicola peyrierasi: Montreuil 2005b: 376; Wirta et al. 2008: 1080, 1081 (phylogeny), 1086 (a ppendix A).

Type material examined. *Holotype*, male: "Madagascar Ouest, réserve spéciale du Zombitsy, Est de Sakaraha, matsabory, 640m, 7-10.II.1974, P. Viette et A. Peyrieras / Holotype Helictopleurus peyrierasi n. sp. R. Paulian et Y. Cambefort det. 1991 / HOLOTYPE" (MNHN).

Paratype, female: same data as holotype, except the collection date: "13.II.1974" (MNHN).

Distribution. This species is known from the central-western coast of Madagascar (Boeny and Menabe regions).

Taxonomic remarks. Paulian and Cambefort (1991) described *H. peyrierasi* from Zombitsy, south-western Madagascar. Montreuil (2005b), after having examined specimens collected in nearby Kirindy, and having compared them with the type specimens of *Helictopleurus fungicola*, treated this taxon as a subspecies of *H. fungicola.* We compared the type specimens of the nominotypical subspecies with those of *H. fungicola peyrierasi* and found significant differences, especially in the shape of male genitalia, that support the original treatment of *H. peyrierasi* stat. rest. as a full species within the genus *Helictopleurus*.

Helictopleurus viettei Paulian & Cambefort, 1984

Figure 3A–E

Helictopleurus viettei Paulian & Cambefort 1984: 113; Montreuil 2005a: 133.

Type material examined. ***Holotype***, female: "Madagascar Ouest, réserve spéciale du Zombitsy, Est de Sakaraha, matsabory, 640m, 13.II.1974, P. viette et A. Peyrieras / Holotype Helictopleurus viettei n. sp. R. Paulian et Y. Cambefort det. 1984 / HOLOTYPE" (MNHN).

Paratype, female: same data as holotype, except the collection date: "7–10. II.1974" (MNHN).

Distribution. Only known from south-western Madagascar (Atsimo-Andrefana region).

Helictopleurus sicardi (Paulian, 1975)

Figure 4A–I

Heterosyphus sicardi Paulian, 1975: 248; Halffter and Edmonds 1982: 136; Paulian and Cambefort 1984: 50 –51; Paulian 1986: 107; Cambefort 1991: plate 4.6 (unpaginated); Paulian and Cambefort 1991: 113; Davis et al. 2002: 1224; Montreuil 2005a: 134; Wirta et al. 2008: 1080–1081 (caption and phylogenetic tree), 1087 (appendix A); Philips 2011: 27; Sole et al. 2011: 3.

Helictopleurus sicardi: Philips, 2016: 11, 13, 40–41 (synonymy *Heterosyphus* = *Helictopleurus*).

Type material examined. ***Lectotype***, female (here designated): "Montagne d'Ambre. I. / Epactoides *nar*? / TYPE / *Heterosyphus sicardi* n.g. n.sp. R. Paulian det. /. Heterosyphus sicardi Paulian, 1975 des. Rossini et al. 2021 / LECTOTYPE. Helictopleurus sicardi (Paulian, 1975) Rossini et al. des. 2021" (MNHN).

Paralectoype, female: "Antsiranana / Madagascar Montagne d'Ambre Muséum Paris Coll. Sicard 1930" (MNHN).

Additional material examined. Madagascar: "Mt. d'Ambre. −12.5281, 49.1709. 1080m. 1.i.2019. sift. MD31. V. Grebennikov, http://id.luomus.fi/NC.01" (1 male MZHF); same data, http://id.luomus.fi/NC.02 (1 female, MZHF; body parts disarticulated); same data, http://id.luomus.fi/NC.03 (1 female MZHF; body parts disarticulated, DNA material); same data (3 males, 7 females, MZHF); "Montagne d´Ambre. Jan 2004. Wet forest. Alt. 1300 m. fish baited trap. Iikka Hanski leg. / http://id.luomus.fi/GZ.19901. I.2004" (1 female, MZHF); same data, "http://id.luomus.fi/GZ.19902. I.2004" (1 male, MZHF).

Diagnosis. Within the endemic Madagascar genus *Helictopleurus*, *H. sicardi* shares a series of morphological characters with the species here assigned to the *fungicola* group. These characters are the posterolateral margin of the pronotum extended in the pro-

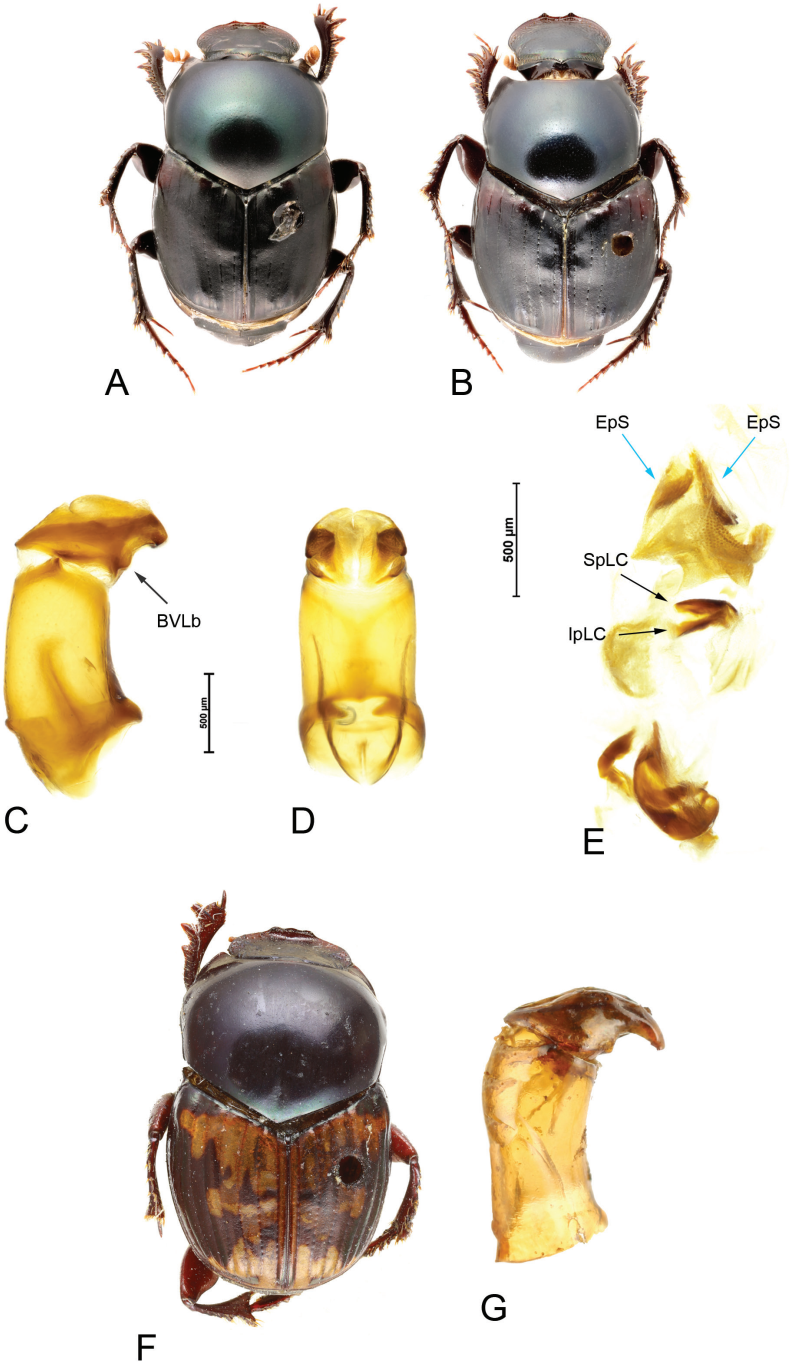

Figure 3. *Helictopleurus viettei* **A, B** habitus of male (**A**) and female (**B**) **C, D** lateral and anterior view of the aedeagus; basoventral lobes (BVLb) **E** endophallus: endophallic spines (EpS); superior (SpLC) and inferior (IpLC) part of the lamella copulatrix. *Helictopleurus pluristriatus* **F** dorsal habitus of the holotype **G** lateral view of the aedeagus.

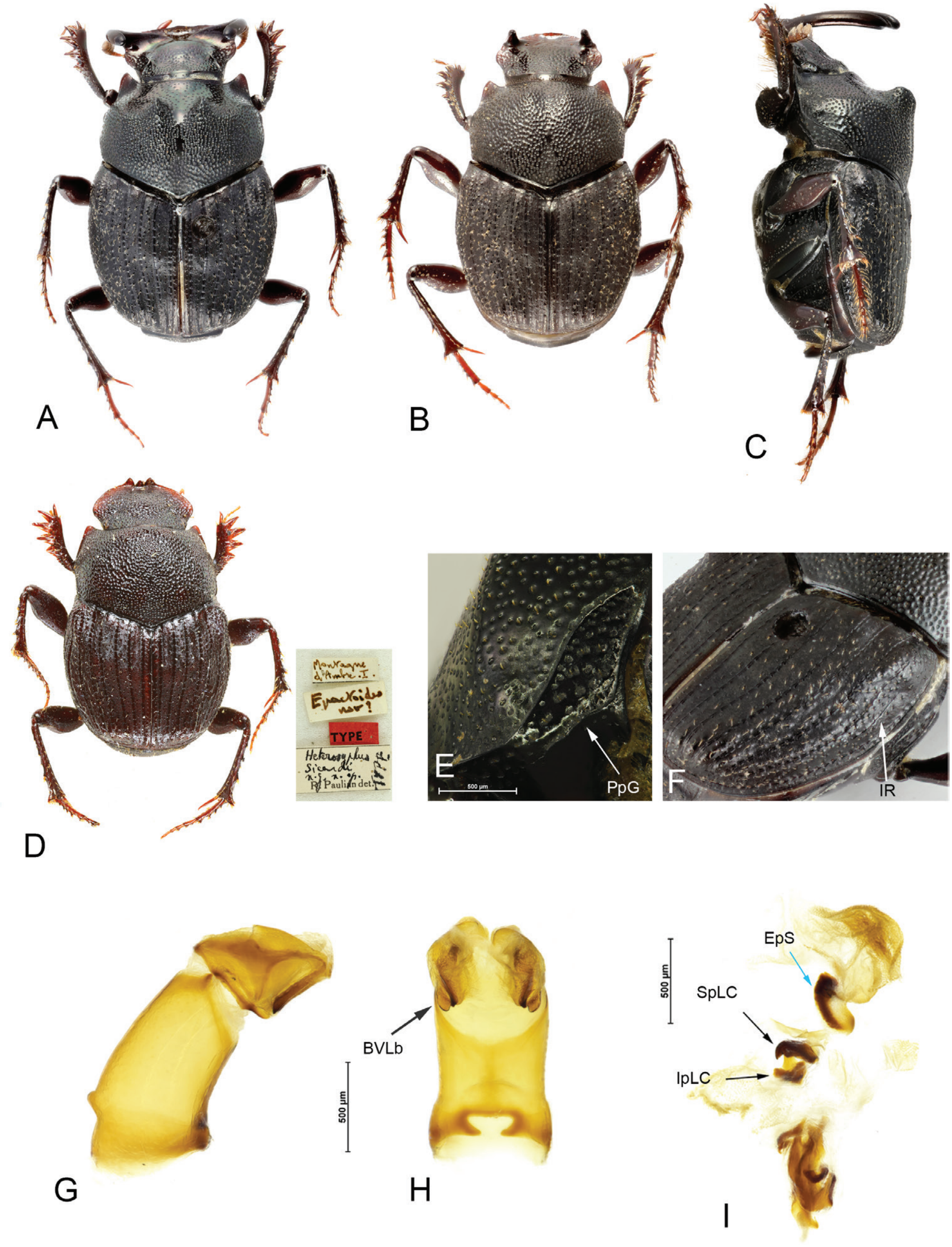

Figure 4. *Helictopleurus sicardi* **A, B** major (**A**) and minor (**B**) male dorsal habitus **C** major male lateral habitus **D** female dorsal habitus (lectotype) and original labels **E** propleural groove (PpG) **F** VIII interstrial ridge (IR) **G, H** lateral and anterior view of the aedeagus; basoventral lobes (BVLb) **I** endophallus: endophallic spines (EpS); superior (SpLC) and inferior (IpLC) part of the lamella copulatrix.

pleural region with a short ridge beneath the lateral edge of the pronotum; clypeal margin of female with acute teeth at middle (three teeth as in *H. fungicola* and *H. peyrierasi*); parameres elongated; lamella copulatrix very simple and composed by a superior and inferior leaf-like parts; and superior side of the membranous sac of the endophallus with regions covered by scale-like spines. However, *H. sicardi* is easily distinguished from the other members of the *fungicola* group by the large punctation on the pronotum (very fine to absent in *H. fungicola*, *H. peyrierasi*, and *H. viettei*); male with a couple of long and widely curved clypeal horns (head unarmed in the remaining species; with an acute to obtuse post-occipital tubercle in *H. peyrierasi*); body completely brown (pronotum and head dark with blue to emerald green sheen, and elytra bicolored with reddish or yellow spots in the other species of the group); and elytra with rows of bright, elongated granules (granules absent in *H. fungicola*, *H. peyrierasi*, and *H. viettei*).

Description of the male. ***Body length and color.*** Body length from clypeal margin to elytral apices 7 mm, dorsal and ventral side of the body brown and bright, dorsal tegument clearly sericeous on the disc of the head, posteromedian region of pronotum and elytral interstriae; mouthparts and antennae light brown, setae light yellow to brownish.

Head. Clypeus with margin widely and evenly curved, with sides straight and parallel in proximity of the horns, genal margin curved, clypeogenal junction indicated by a short and shallow ridge, and by the base of the clypeal horns. Clypeus with two long and widely curved horns (Fig. 1D, 4A, C), with tips rounded and slightly convergent at middle. Horns laterally flattened and basally strongly widened, bases of the horns occupy most of the lateral region of the clypeus. Clypeus smooth and shiny, clypeal disc with scattered and shallow punctures; frons with punctation coarser and denser. Frons without armature, eye opening very narrow and elongated anteroposteriorly. Antennae with eight articles; antennal club small and rounded.

Thorax. In dorsal view, pronotum narrower with respect to elytra, in lateral view slightly convex. Lateral edges rather straight and weakly divergent from posterior angles to the middle, feebly concave and sinuate from middle to anterior angles. Pronotal anterior angles narrow and obtusely acuminate. Lateral and anterior pronotal edges complete and finely margined, posterior edge with no margin. The pronotal posterior edge is extended in the propleura, beneath the lateral edge of the pronotum, with a shallow groove (Fig. 4E). Anterosuperior region of pronotum with two parallel and high carina, anteriorly oriented and separated by a large depression.

Posteromedial pronotal region with punctation rugulose-lacunose and coarse, central and medial region without punctures, punctation more spaced in the anterior region. Several punctures associated with short and stout setae. Pronotal tegument shiny and smooth on anterior half, posterior half finely microsculptured and especially in the middle.

Propleuron weakly excavated at the bottom of the pronotal anterior angles; propleuron with two carinae, the internal carina thinner and straight, external one stronger and widely sinuate.

Episternum very narrow; mesosternal surface covered by coarse and dense punctures associated with short and stout setae, anterior region of mesosternum with a wide and smooth bead, triangularly pointed backward at middle; metasternum wide and steeply elevated with respect to the mesosternum in its superior region, surface smooth, with fine punctures on the disc and coarse punctures near the mesocoxae.

Abdomen. Elytra with eight glossy striae interrupted by a series of well-spaced and shallow punctures. Interstriae flat, with surface completely microreticulated, interstriae III–VI clearly swollen apically (carinated), interstria VIII with a longitudinal, thin ridge on basal one third (Fig. 4F). All interstriae with one to two rows of bright granules not perfectly aligned and unevenly distributed, each granule bears a short seta bowed backward. Humeral callus well developed, elytral surface with a distinct depression nearby the callus.

Sternites ventrally visible, anterior margin with a double row of coarse and shallow punctures not perfectly aligned, three rows of punctures on the lateral most region of each sternite.

Pygidium flattened, completely margined, pygidial surface finely microreticulated and with scattered, shallow punctures.

Legs. Lateral margin of protibiae with four acute teeth distributed along the anterior half, posterior half serrated, apical and internal margin of protibia with an acute spur directed forward and slightly bent downward; ventral side of protibial with a longitudinal ridge that terminates apically with an acute tooth beneath the superior spur. Meso and metatibiae slender, enlarged apically, and respectively with two and one spiniform spurs at the apex. Profemora elongated, dorsal side smooth, ventral side with coarse and shallow punctures mostly concentrated on posterior half. Mesofemora and metafemora very slender and swollen posteriorly at middle, ventral surface with coarse and shallow punctures on posterior half, fine punctures anteriorly.

First segment of mesotarsi with four spine-like teeth in the external margin, two to three yellow setae inserted between each tooth.

Morphological variation. Minor males either with two small and straight clypeal horns that arise from the sides (Fig. 4B) or without horns, the head is subtrapezoidal, and the anterosuperior pronotal carina are absent; the anterior half of the pronotum is feebly depressed longitudinally at middle.

Females differ from males by the clypeal margin with three teeth distinctly reflexed upward, the lateral teeth obtuse, while the central one more acuminated, posterior margin of the lateral teeth with short setae; head surface covered by coarse and shallow punctures even on the clypeus where the punctation is shallower; pronotum not depressed medially; protibia without internoapical tooth; last abdominal sternite narrower at middle.

Male genitalia. Parameres elongated, ventrally defined by two straight laminas, basoventral side of the parameres with two lateral lobes obtusely squared (BVLb, Fig. 4G, H). Lamella copulatrix simple and consisting of a superior (SpLC) and inferior (IpLC) leaf-like part; margin of the superior part with a sharp hook (Fig. 4I). Superior side of the membranous sac of the endophallus covered by a scale-like spines (EpS, Fig. 4I).

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Supplementary material 1

DNA sequence alignment of the material examined in our study

Authors: Michele Rossini, Olivier Montreuil, Vasily Grebennikov, Sergei Tarasov

Data type: molecular data

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Neotropical *Nilothauma* Kieffer, 1921 (Diptera, Chironomidae): Key, eleven new species, re-descriptions, new combination and new records

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Abstract

Nine new species of *Nilothauma* Kieffer, *N. hamadae* **sp. nov.**, *N. jupau* **sp. nov.**, *N. karitiana* **sp. nov.**, *N. leccii* **sp. nov.**, *N. marianoi* **sp. nov.**, *N. mateusi* **sp. nov.**, *N. txukuyana* **sp. nov.**, *N. werekena* **sp. nov.** and *N. yekwana* **sp. nov.** are described and figured, based on adult males collected in Brazil and *N. maya* **sp. nov.** on an adult male from Mexico; *N. terena* **sp. nov.** is described as male, pupa and larva based on a reared specimen from Brazil. *Nilothauma aleta* Roback, 1960 and *N. duena* Roback, 1960 are re-described and recorded from Brazil. *Nilothauma longissimum* Mendes & Andersen, 2009 is transferred to *Beardius* Reiss & Sublette, 1985 and the diagnosis of *Nilothauma* is emended. New records of thirteen Neotropical *Nilothauma* species are given and a key to the males of all known species of *Nilothauma* is provided.

Keywords

Brazil, key, Mexico, Neotropical Region, new combination, new records, new species, taxonomy

Introduction

The genus *Nilothauma* was erected by Kieffer (1921), based on the Afrotropical *N. pictipenne* Kieffer, 1921. The Neotropical genera *Neelamia* Soponis, 1987 and *Paranilothauma* Soponis, 1987 were both placed as synonyms of *Nilothauma* by Mendes and Andersen (2009). Most males of *Nilothauma* can be recognised by having an antenna with 13 flagellomeres, low antennal ratio (except in *Nilothauma longissimum* Mendes & Andersen, 2009), fore-tibia with long spur on conical, apical scale, high venarum ratio and squama bare (Mendes and Andersen 2009). In addition, many males have median or lateral, sometimes strongly setose lobes or projections on tergite IX. The larvae of *Nilothauma* inhabit littoral and sublittoral soft sediments of lakes, streams and rivers (Epler et al. 2013).

To date, the genus comprises 52 described species that occur in all zoogeographical regions, except Antarctica (Qi et al. 2014, 2016; Niitsuma 2016; Dantas and Hamada 2017). A total of 22 species are known from the Neotropical and four from the Nearctic Regions (Andersen et al. 2016; Dantas and Hamada 2017).

After examining material collected in several localities in the Neotropical Region, mostly from the Brazilian Amazon, 24 species of *Nilothauma* were identified. Eleven of them proved to be new to science and are described below as adult males and for *N. terena* sp. nov. also as larva and pupa. The other thirteen species have their distribution range extended in the Neotropics. *Nilothauma aleta* Roback, 1960 and *N. duena* Roback, 1960, originally described from the Peruvian Amazon are re-described, based on material from Brazil and *N. longissimum* Mendes & Andersen, 2009 is transferred to *Beardius* Reiss & Sublette, 1985. A key to the males of all known species of *Nilothauma* is provided.

Material and methods

Alcohol-preserved specimens were dissected and slide-mounted in Euparal. Morphological terminology and abbreviations follow Sæther (1980). Measurements are taken according to Epler (1988) and given as ranges, followed by the mean when more than three specimens were measured, followed by the number of specimens measured in parenthesis.

Abbreviations used in the text as follows:

CEPA	Centro de Estudos e Pesquisas Ambientais (Centre for Environmental Studies and Research);
EB	Estação Biológica (Biological Station);
INPA	Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil);
MZSP	Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil);
PE	Parque Estadual (State Park);
RPPN	Reserva Particular do Patrimônio Natural (Private Natural Heritage Reserve);

UFSC	Entomological Collection of the Federal University of Santa Catarina (Florianópolis, Brazil);
ZMBN	University Museum of Bergen (Bergen, Norway);
ZSM	Zoologische Staatsammlung München (Munich, Germany).

Type material is deposited at INPA, MZSP, UFSC, ZMBN and ZSM, as stated in each description. Vouchers are deposited at UFSC, ZMBN and ZSM.

Taxonomy

Beardius Reiss & Sublette, 1985

Beardius longissimus (Mendes & Andersen, 2009), comb. nov.

Nilothauma longissimum Mendes & Andersen, 2009: 26

Material examined. Type material, as in Mendes and Andersen (2009).

Additional material. 8 males, slide-mounted: Brazil, Bahia, Camacan, RPPN Serra Bonita, Trilha Bapeba,15°20'35"S, 39°33'34"W, 4.xi.2009, light trap, A.R. Calor et al. leg. 3 males, slide-mounted, as previous, except: 15°23'32"S, 39°33'53"W, 2.xi.2009. 1 male, slide-mounted, as previous, except: 03.ii.2009. 1 male, slide-mounted, as previous, except: córrego 2, 15°23'10"S, 39°34'03"W, 819 m a.s.l., 01.viii.2008, light trap, A.R. Calor, L.S. Lecci, L.C. Pinho & R.A. Moretto leg. 1 male, slide-mounted: Brazil, São Paulo, PE Serra do Mar, Ubatuba, Picinguaba, Camburi stream, 09.ix.2006, light trap, M.R. Spies & A.E. Siegloch leg.

Remarks. Pinho et al. (2013) found that the "presence of apical thin setae on inferior volsella" (character 74, state 1), i.e. a group of two, rarely three, slender simple setae at the very tip of the inferior volsella, in addition to subapical, stouter setae, is the only synapomorphy of *Beardius* Reiss & Sublette, 1985 in the adult stage. In fact, the character is shared by all species of *Beardius* and is not found elsewhere, except in *Nilothauma longissimum* Mendes & Andersen, 2009, a species that was considered to be sister to all remaining *Nilothauma* by Mendes and Andersen (2009) in a phylogenetic analysis with *Paratendipes* Kieffer and *Pseudochironomus* Malloch as outgroups. The comparatively-high antennal ratio in *N. longissimum* (AR > 1.00) is the only exception in *Nilothauma*, which generally have very low antennal ratios (AR < 0.40). Further, the venarum ratio (VR) seems to be low in *N. longissimum* compared to other *Nilothauma* species; other characters in *N. longissimum* are consistent with the current diagnosis of *Beardius.* We therefore propose the new combination and emend the diagnosis of *Nilothauma* accordingly.

Distribution. The species was originally described from São Paulo State, south-eastern Brazil by Mendes and Andersen (2009); the range is now extended to Bahia State in north-eastern Brazil.

Nilothauma Kieffer, 1921

Emended diagnosis. After transferring *Nilothauma longissimum* Mendes & Andersen, 2009 to *Beardius* Reiss & Sublette, 1985 (see above), adult males of *Nilothauma* become more easily separated from other genera. The diagnosis given by Mendes and Andersen (2009) has to be emended as follows: "antennal ratio generally low (AR < 0.40), one species (*N. longissimum* sp. nov.) with AR > 1.00." should read: "antennal ratio generally low (AR < 0.40), occasionally as high as 0.82 (*N. soka* Andersen, Bello González & Hagenlund, 2016).

The discovery of the pupae of *N. terena* sp. nov. leads to the diagnosis of the pupa given by Mendes and Andersen (2009) having to be emended as follows: "Frontal setae short, not on tubercles." should read "Frontal setae short, occasionally long and taeniate, not on tubercles." Further, "Sternites I–VII bare; sternite VIII with central, longitudinal field of shagreen." should read "Sternites I–VII usually bare, sternite I occasionally with extensive shagreen; sternite VIII with central, longitudinal field of shagreen."

Based on the larva of *N. terena* sp. nov., the diagnosis of the *Nilothauma* larvae in Epler et al. (2013) should be emended as follows: "Mandible. All teeth pale;" should read: "Mandible. All teeth pale, occasionally inner teeth with somewhat darker pigmentation;" and "Mentum. Pale;" should read: "Mentum. Pale, occasionally with somewhat darker pigmentation".

Nilothauma aleta Roback, 1960

Figures 1A, B, 17B

Additional material. 1 male, slide-mounted: Brazil, São Paulo, São Luís do Paraitinga, PE Serra do Mar, Núcleo Santa Virgínia, trilha Poço do Pito, afluente Paraibuna, 23°20'09"S, 45°08'46"W, 15.ix.2006, light trap, M.R. Spies & A.E. Siegloch leg.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX without setose dorsal lobe(s); gonostylus stout; acrostichals absent; anal point wide, covering most setae along posterior margin of tergite IX; inferior volsella slender.

Re-description. Male imago (n = 1). Total length 3.58 mm. Wing length 2.00 mm. Total length/wing length 1.79. Wing length/length of profemur 2.25.

Colouration. Head, thorax and abdomen brown; legs pale, except for ring of brown pigmentation in distal 1/2 to 2/3 of fore- and hind femora, in distal 1/3 of foretibia, in basal 1/8 of mid- and hind tibiae and in distal 1/3 of each tarsomere. Wing membrane apparently hyaline, but faint brown markings are visible when dark-field filter is applied.

Antenna. AR = 0.27. Thirteenth flagellomere 197 µm long.

Head. Temporal setae 7 in single row. Clypeus with 25 setae. Tentorium 123 µm long, maximum width 25 µm. Stipes not measurable. Palp segment lengths (in µm): 39, 34, 123, 147, 191. Third palpomere with 2 sensilla clavata subapically, longest 20 µm long. Fifth palpomere/third palpomere 1.55.

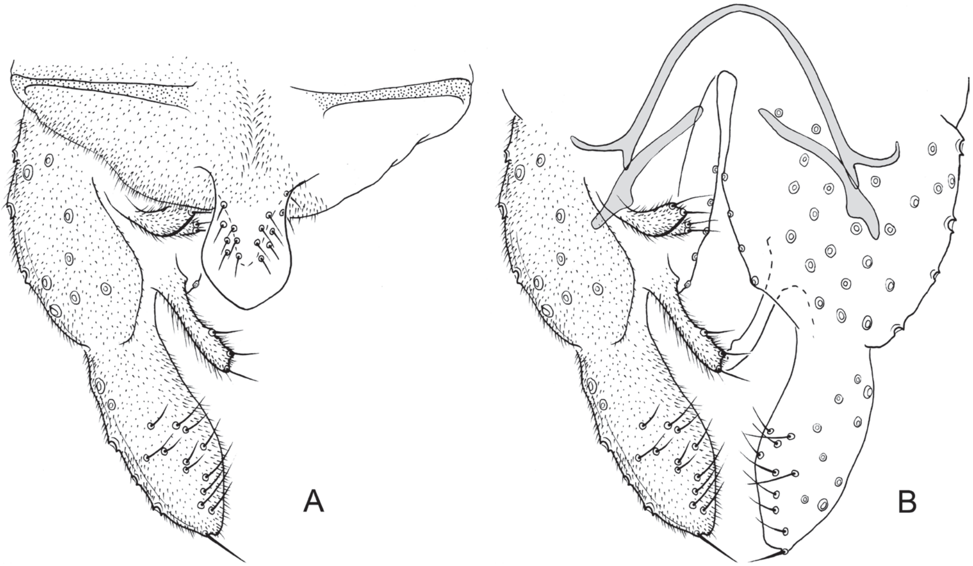

Figure 1. *Nilothauma aleta* Roback, 1960, adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Thorax. Dorsocentrals 12 in single row, acrostichals absent, prealars 3. Scutellum with 6 setae.

Wing. VR = 1.50. Brachiolum with 1 seta, R with 13 setae, R_1 with 18 setae, R_{4+5} with 21 setae, remaining veins bare.

Legs. Spur of fore tibia 44 µm long including 15 µm long scale. Mid-tibia with 1 spur, 15 µm long; hind tibia with 2 spurs, 25 and 29 µm long. Combs of both mid- and hind tibia 20 µm long. Width at apex of fore-tibia 39 µm, of mid-tibia 34 µm, of hind tibia 44 µm. Lengths and proportions of legs as in Table 1.

Hypopygium (Fig. 1A, B). Tergite IX without lobes, tapering to apex, with 22 short setae underneath anal point. Anal point lanceolate, 50 µm long, maximum width 37 µm. Tergite bands well developed. Laterosternite IX without setae. Phallapodeme 70 µm long; transverse sternapodeme 55 µm long. Gonocoxite 134 µm long. Inferior volsella straight, 52 µm long, 7 µm wide medially, with microtrichia and 8 simple setae apically. Superior volsella pediform, 17 µm long, 7 µm wide at base, covered with microtrichia and with 2 setae apically. Median volsella 7 µm long, with 2 simple setae, longest 12 µm. Gonostylus 95 µm long, straight. HR = 1.42. HV = 3.77.

Female adult and immatures. Unknown.

Remarks. Roback (1960) described *Nilothauma aleta* Roback, 1960 and *N. duena* Roback, 1960 from the Peruvian Amazon. In their revision of *Nilothauma*, Adam & Sæther, (1999) regarded the two species as not belonging to *Nilothauma* since they lack any projections on tergite IX and stated that they appear to belong in *Paratendipes* Kieffer. Later, Mendes and Andersen (2009) placed *Neelamia* Soponis and *Paranilothauma* Soponis as synonyms of *Nilothauma* and several new Neotropical species have been described demonstrating the large morphological variation in the genus. Mendes

Table 1. Lengths (in µm) and proportions of leg segments in *Nilothauma aleta* Roback, 1960, adult male (n = 1).

	Fe	Ti	ta_1	ta_2	ta_3	ta_4
p_1	887	601	837	522	404	256
p_2	906	690	414	227	177	118
p_3	1034	985	699	355	305	197
	ta_5	**LR**	**BV**	**SV**	**BR**	
p_1	148	1.39	1.74	1.77	2.3	
p_2	89	0.60	3.29	2.30	2.3	
p_3	108	0.71	2.56	2.89	5.0	

and Andersen (2009) emended the diagnosis of *Nilothauma* and both *N. aleta* and *N. duena* fit well into this diagnosis.

Distribution (Fig. 17B). The species was originally described from the Department of Huánuco, in the Peruvian Amazon by Roback (1960); the range is now extended to Serra do Mar (São Paulo State), in the Brazilian Atlantic Forest.

Nilothauma amazonense Mendes & Andersen, 2009

Figure 17A

Additional material. 1 male, slide-mounted: Brazil, Santa Catarina, Grão Pará, Cachoeira do Amado, #27, 28°08'57"S, 49°21'17"W, 16.xi.2012–08.i.2013, Malaise trap, L.C. Pinho, M.C. Novaes & M.F. Haddad leg. 1 male, slide-mounted: Brazil, Santa Catarina, São Francisco do Sul, Distrito do Saí, 26°11'42"S, 48°43'53"W, 18.i–18.iii.2020, Malaise trap #150, small stream, L.C. Pinho et al. leg.

Remarks. *Nilothauma amazonense* Mendes & Andersen, 2009 was described, based on a single male from the Amazon. The specimens of *N. amazonense* from southern Brazil, however, differ slightly from the holotype. Mendes and Andersen (2009) stated that hind ta_2 being shorter than ta_3 (ratio of ta_2/ta_3 length = 0.73) is one of the diagnostic characters of the species. However, in the specimens from southern Brazil, hind ta_2 and ta_3 are subequal in length (ratio of ta_2/ta_3 length = 0.94–0.97). Body size, measured as Total Length (TL) is also larger (TL of holotype = 1.53 mm; TL of southern populations = 2.00–2.05 mm). Similar differences in body size between Amazonian and southern Atlantic Forest populations were also found in *Beardius urupeatan* Pinho, Mendes & Andersen, 2009 [TL Amazon = 2.32–2.51, 2.38 (6); TL southern Atlantic Forest = 2.68–3.00, 2.96 (8)]. This intraspecific variation might be due to the higher temperature in the Amazon Region when compared to the localities in the southern parts of the Atlantic Forest. Populations of chironomid species inhabiting different habitats may show variation in voltinism and more rapid growth can result in smaller body size (Tokeshi 1995; Pinho et al. 2009).

Distribution (Fig. 17A). The species was originally described from the Amazonian Region by Mendes and Andersen (2009); the range is now extended to Santa Catarina State in southern Brazil.

Nilothauma anamariae Dantas & Hamada, 2017

Figure 17D

Additional material. 1 male, slide-mounted: Brazil, Rondônia, Candeias do Jamari, Rio Preto, Ponte de Madeira, #01, 08°52'40"S, 63°38'02"W, 19–20.vii.2012, light trap, R. Boldrini & A.S. Fernandes leg. 1 male, slide mounted: Brazil, Mato Grosso, Ribeirão Cascalheira, Fazenda Campina Grande, Rio Suiá Miçu, 28–30.xi.2006, light trap, A.R. Calor, F.R. Silva & S. Mateus leg. 2 males, slide-mounted: Brazil, Mato Grosso, Ribeirão Cascalheira, Fazenda Campina Verde, Rio Suiá Miçu, 12°48.591'S, 52°06.925'W, 10.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg. 1 male, slide-mounted: Brazil, Pará State, Rurópolis, Rio Tambor, 29.x.2007, light trap, N. Hamada et al. leg.

Remarks. The inferior volsella can have up to 3–4 simple, curved setae apically.

Distribution (Fig. 17D). The species was originally described from the Rio Grande do Sul State in southern Brazil by Dantas and Hamada (2017); the range is now extended to Mato Grosso, Rondônia and Pará States in central and northern Brazil.

Nilothauma aripuanense Mendes & Andersen, 2009

Figure 17B

Additional material. 2 males, slide-mounted: Brazil, Rondônia, Candeias do Jamari, Rio Preto, Ponte de Madeira, #01, 08°52'40"S, 63°38'02"W, 19–20.vii.2012, light trap, R. Boldrini & A.S. Fernandes leg. 2 males, slide-mounted: Brazil, Rondônia, Teixeirópolis, Balneário com Cachoeira, 10°55'20"S, 62°22'34"W, 03.ix.2012, light #13, N. Hamada, R. Boldrini, A.S. Fernandes & J.M. Cavalcante leg. 1 male, slide-mounted: Brazil, Roraima, Boa Vista, Rio Cauamé, 02°52'06"N, 60°44'24"W, 9.iii.2009, light trap, L.M. Fusari leg. 1 male, slide-mounted: Brazil, Roraima, Boa Vista, BR-174, Igarapé Água Boa, 02°43'32"N, 60°48'43"W, 2014, N. Hamada leg. 1 male, slide-mounted: Brazil, Amazonas, Presidente Figueiredo, AM-240 Km 20, Balneário Sossego da Pantera, Igarapé da Onça, 02°02'31"S, 59°51'05"W, 02.vii.2008, light trap, C. Azevedo leg. 1 male, slide-mounted: Brazil, Amazonas, upper Rio Marauiá, downstream of Cachoeira Santo Antônio, surface float skimmed, 22.i.1963, E.J. Fittkau leg. (A485, ZSM).

Distribution (Fig. 17B). The species was originally described from the Amazonas and Mato Grosso States by Mendes and Andersen (2009); the range is now extended to Roraima and Rondônia States in the Brazilian Amazon.

Nilothauma calori Mendes & Andersen, 2009

Figures 2A, 16C

Additional material. 1 male, slide-mounted: Brazil, Amazonas, Manaus, Reserva Florestal Adolfo Ducke, Igarapé Bolívia, 02°49'15"S, 59°56'31"W, 9–12.xi.2008,

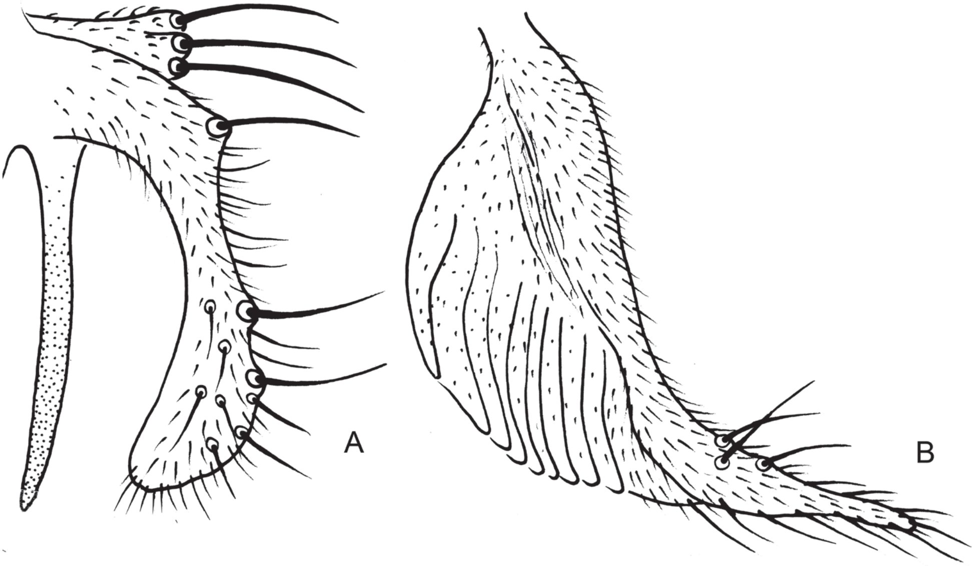

Figure 2. Variation in superior volsella **A** dorsolateral view of superior volsella of *Nilothauma calori* Mendes & Andersen, 2009 **B** lateral view of superior volsella of *Nilothauma complicatum* Mendes & Andersen, 2009.

Malaise trap suspensa 2, N. Hamada et al. leg. 2 males, slide-mounted: Brazil, Mato Grosso, Cuiabá, 10–11.x.1965, Brundin net, E.J. Fittkau leg. (A 580, ZSM).

Remarks. Mendes and Andersen (2009) stated that the superior volsella has a "lateral strongly sclerotized, spine-like projection". In dorsolateral view (Fig. 2A), it can be seen that this spine-like projection originates from the base of the volsella and is equally long as the volsella proper.

Distribution (Fig. 16C). The species was originally described from Acre State by Mendes and Andersen (2009); the range is now extended to the Mato Grosso and Amazonas States.

Nilothauma complicatum Mendes & Andersen, 2009

Figures 2B, 16A

Additional material. 1 male, slide-mounted: Brazil, Rondônia, Candeias do Jamari, Rio Preto, Ponte de Madeira, #01, 08°52'40"S, 63°38'02"W, 19–20.vii.2012, light trap, R. Boldrini & A.S. Fernandes leg. 3 males, slide-mounted: Brazil, Mato Grosso, Nova Xavantina, Fazenda Sr. Queté, Córrego Voadeira, 14°32.187'S, 52°30.902'W, 16.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg. 2 males, slide-mounted, as previous, except: Córrego Cachoeira, 14°32.817'S, 52°31.395'W. 1 male, slide-mounted, as previous, except: 14°41.577'S, 52°27.203'W, 13.x.2007. 2 males, slide-mounted, as previous, except: Estrada p/ Rancho Helena, Córrego Ponte de

Pedra, 14°47.908'S, 52°37.226'W, 15.x.2007. 1 male, slide-mounted, as previous, except: Córrego Voadeira, 14°41.577'S, 52°27.203'W, 13.x.2007. 1 male, slide-mounted: Brazil, Mato Grosso, Ribeirão Cascalheira, Estrada Fazenda Manaus, 1° afluente Rio Bonito, 12°57.088'S, 51°52.480'W, 08.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg.

Remarks. Mendes and Andersen (2009) stated that the superior volsella has a "marginal row of flattened setae". In lateral view (Fig. 2B), it can be seen that the volsella is quite wide medially with a row of lamellae apparently covered with weak microtrichia.

Distribution (Fig. 16A). The species was originally described by Mendes and Andersen (2009), based on a single male from the Espírito Santo State; the range is now extended to the Mato Grosso and Rondônia States in central and northern Brazil.

Nilothauma duena Roback, 1960

Figures 3A, B, 16C

Additional material. 1 male, slide-mounted: Brazil, Bahia, Camacan, Fazenda do Waldemar da farmácia, Córrego abaixo da represa de abastecimento, 15°25'16"S, 39°33'57"W, 300 m a.s.l., 05.viii.2008, light trap, A.R. Calor, L.S. Lecci, L.C. Pinho & R.A. Moretto leg. 1 male, slide-mounted: Brazil, São Paulo, Pindamonhangaba, Fazenda São Sebastião, Afluente Cedro 3, 22°50'16"S, 45°28'27"W, 18.ix.2006, light trap, M.R. Spies & A.E. Siegloch leg.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX without setose dorsal lobe(s); anal point slightly spatulate; wing unmarked; abdominal tergites I–VIII with basal half light brown, distal half pale; gonostylus and inferior volsella stout.

Re-description. Male imago (n = 2, unless otherwise stated). Total length 2.37–2.76 mm. Wing length 1.56–1.68 mm. Total length/wing length 1.58–1.66. Wing length/length of profemur 2.60–2.62.

Colouration. Head and thorax light brown; legs pale except for brown pigmentation in basal 1/3 and distal 1/5 of fore femur, basal 1/5 and distal 1/3 of fore tibia, distal 1/8 of mid- and hind femora, basal 1/8 and distal 1/8 of mid- and hind tibiae and entire tarsi. Abdominal tergites I–VIII with basal half light brown, distal half pale; hypopygium light brown. Wing membrane hyaline.

Antenna. AR = 0.17–0.18. Thirteenth flagellomere 108–118 µm long.

Head. Temporal setae 9–10 in single row. Clypeus with 13–15 setae. Tentorium 98 (1) µm long, maximum width 20 (1) µm. Stipes not measurable. Palp segment lengths (in µm): 17–25, 17–25, 32 (1), 35 (1), 62 (1). Third palpomere with 2 sensilla clavata subapically, longest 15 µm long. Fifth palpomere/third palpomere 1.92 (1).

Thorax. Dorsocentrals 16–17 in single row, acrostichals 14–16, prealars 3. Scutellum with 2–3 setae.

Wing. VR = 1.55–1.56. Brachiolum with 1 seta, R with 12–13 setae, R_1 with 16–17, R_{4+5} with 5–22 setae, remaining veins bare.

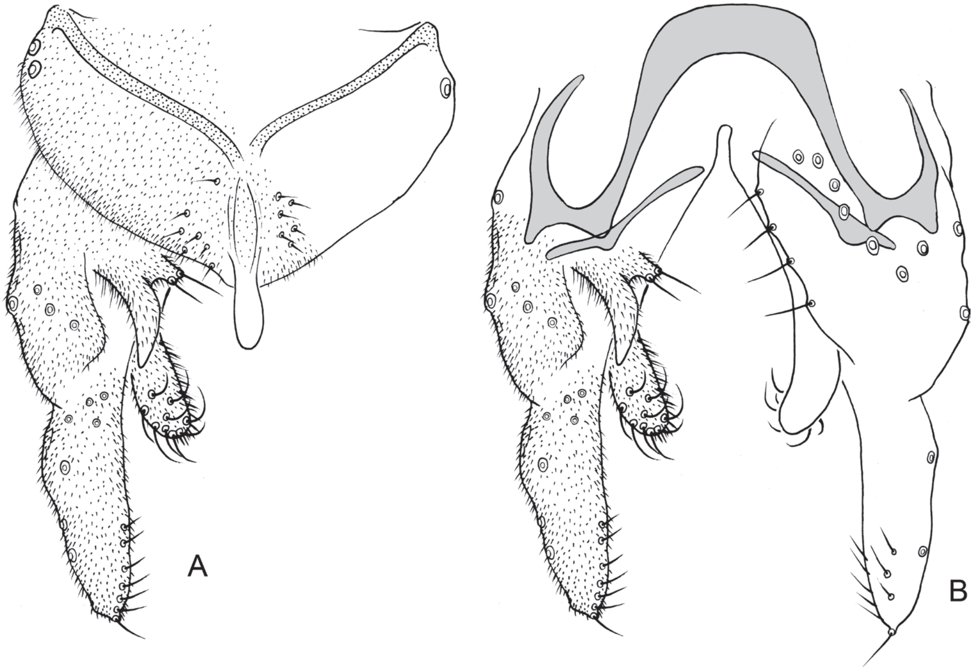

Figure 3. *Nilothauma duena* Roback, 1960, adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Legs. Spur of fore tibia 54–59 µm long including 15–20 µm long scale. Mid-tibia with 1 spur, 25–29 µm long; hind tibia with 2 spurs, 49–51 and 28–31 µm long. Combs of mid-tibia 15–20 µm long, of hind tibia 18–25 µm long. Width at apex of fore tibia 48–50 µm, of mid-tibia 48–50 µm, of hind tibia 49–59 µm. Lengths and proportions of legs as in Table 2.

Hypopygium (Fig. 3A, B). Tergite IX without dorsal lobes, with triangular posterior margin with 13–15 weak setae along posterior margin to each side of base of anal point. Anal point spatulate, 22–30 µm long, maximum width 10–12 µm. Tergite bands well developed. Laterosternite IX with 1–2 setae. Phallapodeme 47–60 µm long; transverse sternapodeme 55–62 µm long. Gonocoxite 112–125 µm long. Inferior volsella straight, 40–45 µm long, 15–20 µm wide medially, with microtrichia and 10–11 strong, simple setae apically. Superior volsella tapering to apex, 20–37 µm long, 12–14 µm wide at base, covered with microtrichia and apparently bare at tip. Median volsella 7–10 µm long, with 3–4 setae, longest 20–22 µm long. Gonostylus 87–90 µm long, straight. HR = 1.29–1.43. HV = 2.72–3.17.

Female adult and immatures. Unknown.

Remarks. See remarks for *N. aleta* Roback, 1960.

Distribution (Fig. 16C). The species was originally described by Roback (1960) from the Department of Huánuco, in the Peruvian Amazon; the range is now extended to Serra Bonita (Bahia State) and Serra do Mar (São Paulo State), in the Brazilian Atlantic Forest.

Table 2. Lengths (in µm) and proportions of leg segments in *Nilothauma duena* Roback, 1960, adult males (n = 2).

	Fe	Ti	ta$_1$	ta$_2$	ta$_3$	ta$_4$
p$_1$	601–640	453–502	660–690	374–376	276–278	207–217
p$_2$	621–670	453–473	296–305	148–158	108–110	69–79
p$_3$	739–778	670–699	404–443	217–236	207–210	148–150
	ta$_5$	**LR**	**BV**	**SV**	**BR**	
p$_1$	105–108	1.37–1.46	1.72–1.74	1.60–1.66	1.8–2.7	
p$_2$	49–59	0.65–0.66	3.48–3.49	3.56–3.74	1.8–2.7	
p$_3$	79–99	0.60–0.63	2.78–2.79	3.33–3.49	3.6–4.7	

Nilothauma fittkaui (Soponis, 1987)

Figure 17A

Additional material. 2 males, slide-mounted: Brazil, São Paulo, Campos do Jordão, PE Campos do Jordão, Córrego Canhambora, 1538 m a.s.l., 22°41'44"S, 45°29'30"W, 13.i.2006, light trap, M.R. Spies leg. 1 male, slide-mounted, Costa Rica, La Selva, 03.iv.1993, Malaise trap, O.A. Sæther leg.

Distribution (Fig. 17A). The species was described by Soponis (1987) from Amazonas and later recorded from Acre, Espírito Santo and Para States in Brazil and from Ecuador by Mendes and Andersen (2009). The range is now extended south to São Paulo State in Brazil and north to Costa Rica in Central America.

Nilothauma hamadae sp. nov.

http://zoobank.org/40ABE99F-793E-4688-9F2E-4D8B21B15E37

Figures 4A, B, 16A

Type material. ***Holotype*** male, slide-mounted: Brazil, Amazonas, Barcelos, Rio Aracá, Foz do Igarapé Cuieiras, 00°19'15"N, 63°16'15"W, 35 m a.s.l., 30.vii–01.viii.2009, light trap #11, N. Hamada et al. leg. (UFSC).

Etymology. The specific epithet is a noun in the genitive case which honours Neusa Hamada for her great contribution to the knowledge of Amazonian Chironomidae.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX with single, median setose dorsal lobe, consisting of a low, but wide protuberance with about 25 strong setae; anal point very broad (about half the width of tergite IX) and lanceolate; median volsella separated from superior volsella.

Description. Male imago (n = 1). Total length 1.94 mm. Wing length 1.13 mm. Total length/wing length 1.71. Wing length/length of profemur 2.30.

Colouration. Head, thorax and abdomen medium brown. Legs light brown. Wing membrane hyaline.

Antenna. AR = 0.40. Thirteenth flagellomere 217 µm long.

Head. Temporal setae 7 in single row. Clypeus with 15 setae. Tentorium 75 µm long, maximum width 12 µm. Stipes 92 µm long. Palp segment lengths (in µm): 25,

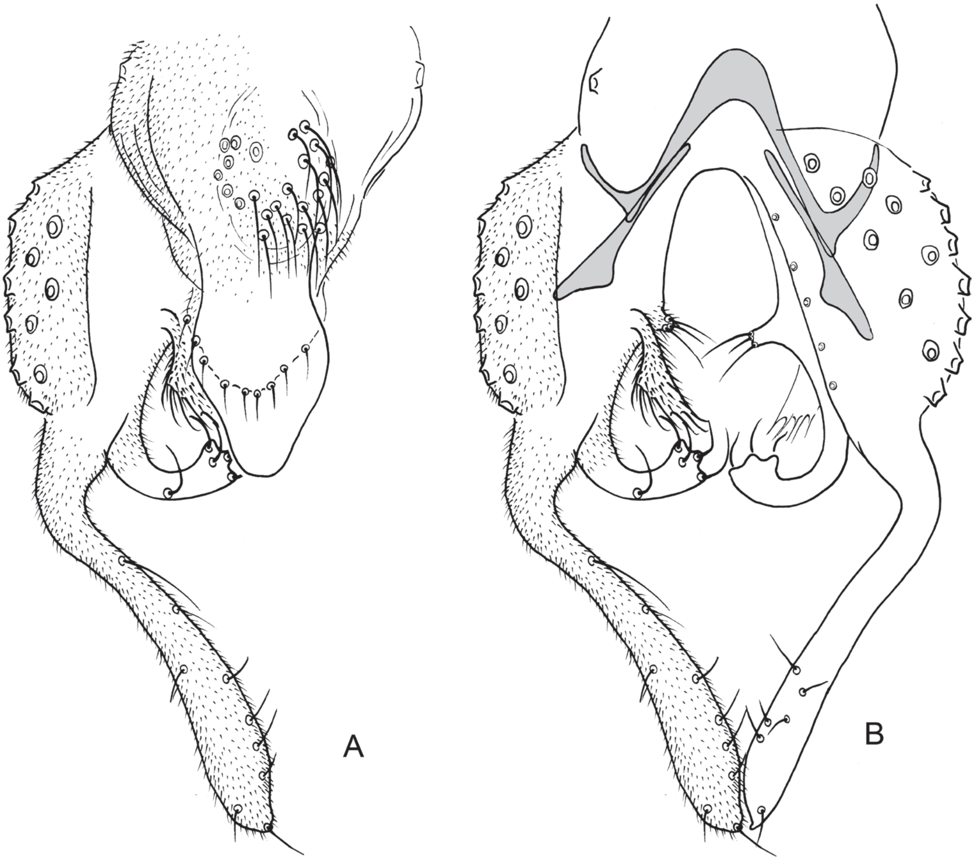

Figure 4. *Nilothauma hamadae* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

25, 75, 127, 144. Third palpomere with 2 sensilla clavata subapically, longest 20 µm long. Fifth palpomere/third palpomere 1.93.

Thorax. Dorsocentrals 7 in single row, acrostichals 10, prealars 2. Scutellum with 4 setae.

Wing. VR = 1.37. Brachiolum with 1 seta, R with 13 setae, R_1 with 7 setae, R_{4+5} with 14 setae, remaining veins bare.

Legs. Spur of fore tibia 34 µm long including 12 µm long scale. Mid-tibia with 1 spur, 15 µm long; hind tibia with 2 spurs, 20 and 25 µm long. Combs of mid-tibia 12 µm long, of hind tibia 15 µm long. Width at apex of fore tibia 34 µm, of mid-tibia 34 µm, of hind tibia 39 µm. Lengths and proportions of legs as in Table 3.

Hypopygium (Fig. 4A, B). Tergite IX narrow, tapering to apex, with central rounded lobe bearing 25 simple, strong setae; with 9 simple setae along posterior margin underneath the anal point. Anal point lanceolate, 42 µm long, 27 µm wide. Tergite bands lacking. Laterosternite IX with 1 seta. Phallapodeme 40 µm long; transverse sternapodeme 15 µm long. Gonocoxite 75 µm long. Inferior volsella strongly curved,

Table 3. Lengths (in µm) and proportions of leg segments in *Nilothauma hamadae* sp. nov., adult male (n = 1).

	Fe	**Ti**	**ta_1**	**ta_2**	**ta_3**	**ta_4**
p_1	493	364	–	–	–	–
p_2	473	364	217	108	79	49
p_3	532	542	315	167	158	99
	ta_5	**LR**	**BV**	**SV**	**BR**	
p_1	–	–	–	–	–	
p_2	49	0.59	3.62	3.86	3.3	
p_3	69	–	–	–	5.0	

37 µm long, 7 µm wide medially, with microtrichia in basal half, with 4 simple setae apically and 1 simple seta subapically. Superior volsella 30 µm long, 4 µm wide at base, covered with microtrichia and fringed at apex. Median volsella 7 µm long, with 2 simple setae, longest 10 µm. Gonostylus 112 µm long, with basal half strongly curved and distal half straight. HR = 0.67. HV = 1.73.

Female adult and immatures. Unknown.

Distribution (Fig. 16A). Known from Barcelos (Amazonas State), in the Brazilian Amazon.

Nilothauma jaraguaense Mendes & Andersen, 2009

Figure 17D

Additional material. 1 male, slide-mounted: Brazil, São Paulo, Salesópolis, EB Boraceia, Rio Claro, Poço Verde, 18.ix.2002, light trap, A.S. Melo, C.G. Froehlich, R. Mariano, A. Prather & R. Blahnik leg. 1 male, slide-mounted: Brazil, São Paulo, Jundiaí, PE Serra do Japi, 23.ix.2008, light trap, R. Mariano & L.S. Lecci leg.

Distribution (Fig. 17D). The species was described by Mendes and Andersen (2009), based on a single male from Parque Estadual do Jaraguá in São Paulo State, Brazil.

Nilothauma jupau sp. nov.

http://zoobank.org/3F55ECB7-8CFC-4229-B33A-3FD9520A23B0

Figures 5A–C, 16A

Type material. ***Holotype*** male, slide-mounted: Brazil, Rondônia, Teixeirópolis, Balneário com Cachoeira, 10°55'20"S, 62°22'34"W, 03.ix.2012, light trap #13, N. Hamada, R. Boldrini, A.S. Fernandes & J.M. Cavalcante leg. (UFSC). ***Paratype*:** 1 male, slide-mounted, same data as holotype (INPA).

Etymology. The specific epithet honours the Jupaú, indigenous people from Rondônia State, Brazilian Amazon. The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX with thorn and without setose dorsal lobe(s); anal point

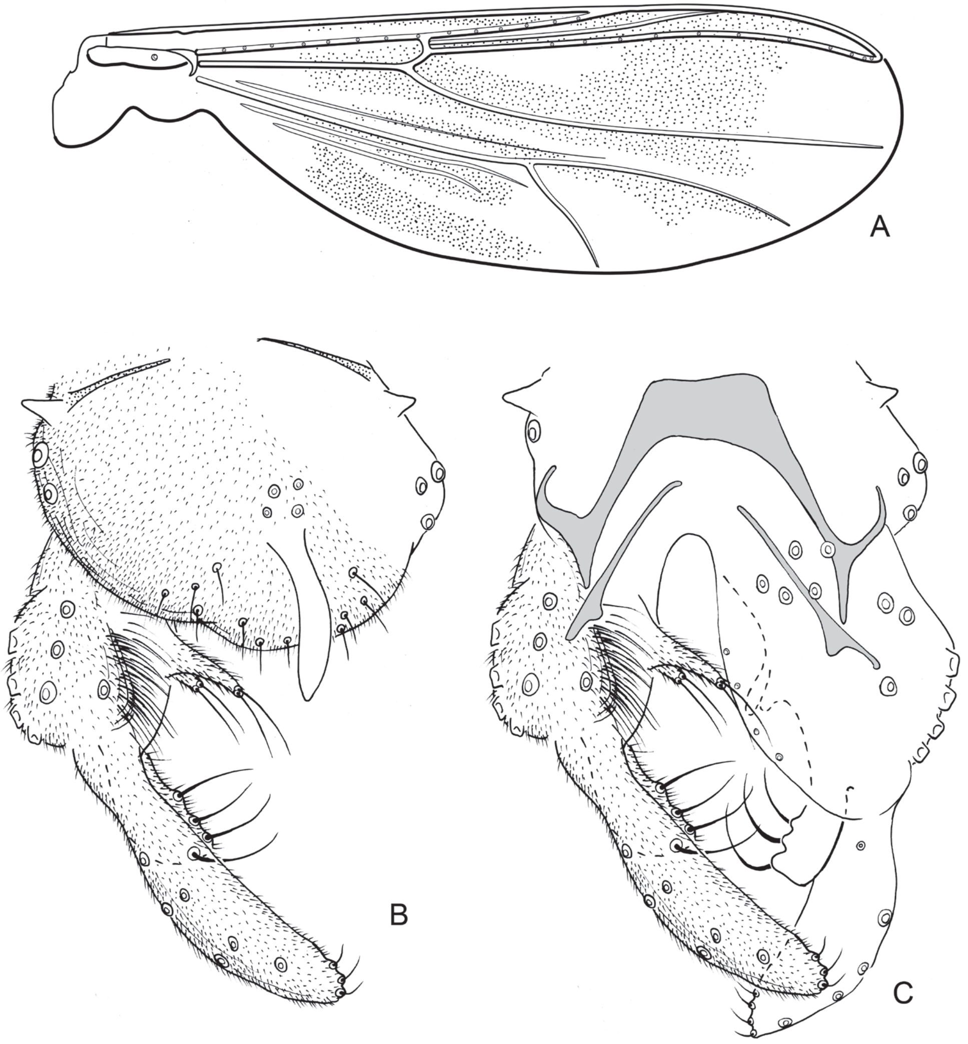

Figure 5. *Nilothauma jupau* sp. nov. adult male **A** wing **B** hypopygium, dorsal view **C** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

spatulate; wing with conspicuous dark markings; abdominal tergites II, III, VI, VII and VIII dark brown.

Description. Male imago (n = 2, unless otherwise stated). Total length 2.04–2.14 mm. Wing length 1.07–1.14 mm. Total length/wing length 1.78–2.01. Wing length/length of profemur 2.03–2.27.

Colouration. Head and thorax brown; legs pale, except for entire fore femur, distal half of mid- and hind femora and distal 1/3 of fore- and hind tibiae with brown pigmentation; abdomen pale, except for brown pigmentation in segments II, III, VI, VII and VIII. Wing membrane with extensive dark markings.

Antenna. AR = 0.28–0.32. Thirteenth flagellomere 115–134 µm long.

Table 4. Lengths (in µm) and proportions of leg segments in *Nilothauma jupau* sp. nov., adult males (n = 2).

	Fe	Ti	ta_1	ta_2	ta_3	ta_4
p_1	502–522	404–424	–	–	–	–
p_2	483–522	335–345	180–187	87–89	57–59	37–39
p_3	542–571	512–522	270–276	138–148	138–148	85–89
	ta_5	**LR**	**BV**	**SV**	**BR**	
p_1	–	–	–	–	–	
p_2	28–30	0.54–0.56	3.22–3.31	4.22–4.56	1.8–2.8	
p_3	59–69	0.53–0.54	2.93–3.23	3.82–3.96	1.5–3.2	

Head. Temporal setae 7–8 in single row. Clypeus with 20–24 setae. Tentorium 57–72 µm long, maximum width 15–17 µm. Stipes 95–100 µm long. Palp segment lengths (in µm): 13–14, 30–32, 85–95, 105–117, 115–134. Third palpomere with 2–3 sensilla clavata subapically, longest 14–15 µm. Fifth palpomere/third palpomere 1.21–1.69.

Thorax. Dorsocentrals 6–7 in single row, acrostichals 8–14, prealars 2. Scutellum with 2 setae.

Wing (Fig. 5A). VR = 1.63–1.64. Brachiolum with 1 seta, R with 8–10 setae, R_1 with 6 setae, R_{4+5} with 11–15 setae, remaining veins bare.

Legs. Spur of fore tibia 39–49 µm long including 20–25 µm long scale. Mid-tibia with 1 spur, 20–25 µm long; hind tibia with 2 spurs, 20–25 and 23–28 µm long. Combs of mid-tibia 15–20 µm long, of hind tibia 15–20 µm long. Width at apex of fore tibia 44 µm, of mid-tibia 39–44 µm, of hind tibia 47–51 µm. Lengths and proportions of legs as in Table 4.

Hypopygium (Fig. 5B, C). Tergite IX without dorsal lobes, with rounded posterior margin, with 4–5 clustered setae anteriorly to base of anal point and 8–12 weaker setae to each side of anal point. Anal point spatulate, 40–42 µm long, maximum width 7–10 µm. Tergite bands well developed. Laterosternite IX with 2–3 setae, with thorn. Phallapodeme 42–52 µm long; transverse sternapodeme 20–22 µm long. Gonocoxite 70–75 µm long, with longer microtrichia dorsomedially. Inferior volsella slightly curved, 30–32 µm long, 15–18 µm wide medially, with microtrichia and 5–6 simple setae in apical one third. Superior volsella slender, 12–20 µm long, 4–5 µm wide at base, covered with microtrichia and with 2 setae at apex, longest 8–13 µm. Median volsella consisting of small tubercle situated underneath superior volsella, 6–7 µm long, with 2 setae at apex, longest 6–7 µm long. Gonostylus 70–92 µm long, straight. HR = 0.81–1.00. HV = 2.21–3.05.

Female adult and immatures. Unknown.

Distribution (Fig. 16A). Known from Rondônia State, Brazilian Amazon.

Nilothauma karitiana sp. nov.

http://zoobank.org/20FE2D58-13AD-47D5-9414-9EB6B7BFC321

Figures 6A–C, 16C

Type material. ***Holotype*** male, slide-mounted: Brazil, Rondônia, Candeias do Jamari, Rio Preto, Ponte de Madeira, 08°52'40"S, 63°38'02"W, 19–20.vii.2012, light

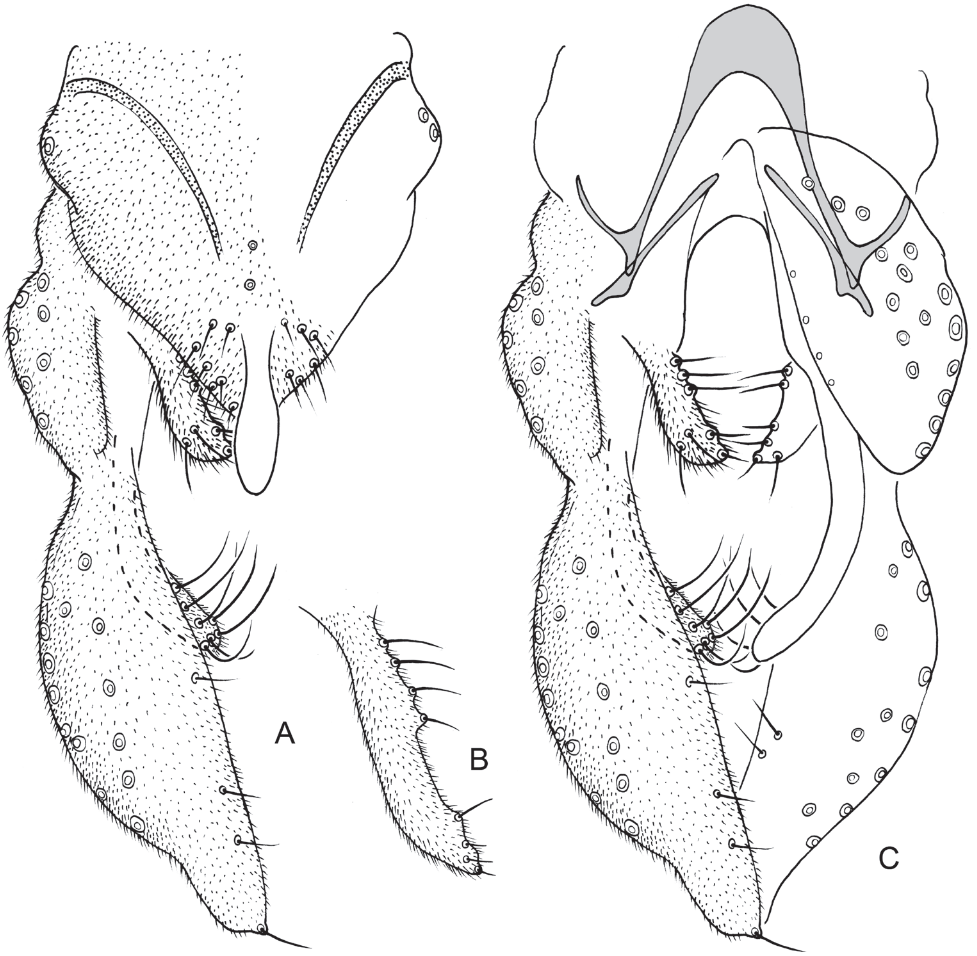

Figure 6. *Nilothauma karitiana* sp. nov. adult male **A** hypopygium, dorsal view **B** superior volsella, dorsal view **C** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

trap #01, R. Boldrini & A.S. Fernandes leg. (UFSC). ***Paratype*:** 1 male adult, slide-mounted: BRAZIL, Amazonas, Barcelos, Rio Aracá, #9, 69 m a.s.l., 00°24'39"N, 63°23'12"W, 28.vii–06.viii.2009, light trap #3, N. Hamada et al. leg. (INPA).

Etymology. The specific epithet honours the Karitiana, indigenous people from the Rio Jamari Basin in the Rondônia State (Brazil). The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX without setose dorsal lobe(s); anal point spatulate; wing unmarked; superior volsella fused to median volsella; gonostylus very long, narrow basally and apically, swollen medially.

Table 5. Lengths (in µm) and proportions of leg segments in *Nilothauma karitiana* sp. nov., adult males (n = 1–2).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**	**ta$_3$**	**ta$_4$**
p$_1$	847–887	729–808	1054	542	424	335
p$_2$	739–798	532–561	374	158	108	69
p$_3$	896–965	867–926	493–522	246–256	240–246	144–148
	ta$_5$	**LR**	**BV**	**SV**	**BR**	
p$_1$	138	1.30	1.91	1.61	2.2	
p$_2$	49	0.67	4.51	3.63	3.2	
p$_3$	95–99	0.56–0.57	3.01–3.27	3.58–3.62	4.0–5.0	

Description. Male imago (n = 2, unless otherwise stated). Total length 3.32–3.78 mm. Wing length 1.71–1.83 mm. Total length/wing length 1.94–2.07. Wing length/length of profemur 2.02–2.06.

Colouration. Head, thorax, legs and abdomen uniformly light brown. Wing membrane hyaline.

Antenna. AR = 0.22 (1). Thirteenth flagellomere 217 µm long.

Head. Temporal setae 9 (1) in single row. Clypeus with 10–11 setae. Tentorium 105 (1) µm long, maximum width 17 (1) µm. Stipes 122 (1) µm long. Palp segment lengths (in µm): 25–35, 27–37, 60 (1), 80 (1), 154 (1). Third palpomere with 3 (1) sensilla clavata subapically, longest 20 (1) µm long. Fifth palpomere/third palpomere 2.57

Thorax. Dorsocentrals 9–13 in single row, acrostichals 12, prealars 2–3. Scutellum with 2 setae.

Wing. VR = 1.33–1.46. Brachiolum with 1 seta, R with 11–14 setae, R$_1$ with 10–12 setae, R$_{4+5}$ with 3–4 setae at apex, remaining veins bare.

Legs. Spur of fore tibia 59–64 µm long including 17–20 µm long scale. Mid-tibia with 1 spur, 23–25 µm long; hind tibia with 2 spurs, 23–25 and 29–33 µm long. Combs of mid-tibia 15–20 µm long, of hind tibia 20–23 µm long. Width at apex of fore tibia 59 µm, of mid-tibia 59 µm, of hind tibia 64 µm. Lengths and proportions of legs as in Table 5.

Hypopygium (Fig. 6A, B). Tergite IX without dorsal lobes, tapering to apex, with 2–3 median and 8–9 setae to each side of anal point. Anal point spatulate, 55–57 µm long, 17–20 µm wide. Tergite bands well developed. Laterosternite IX with 1–2 setae. Phallapodeme 82–90 µm long; transverse sternapodeme 42–55 µm long. Gonocoxite 138–142 µm long. Inferior volsella slightly curved, 97–107 µm long, 17–20 µm wide medially, with microtrichia and 6–7 simple setae subapically. Superior volsella digitiform, 55–65 µm long, 17–20 µm wide at base, covered with microtrichia and with 4 setae apically. Median volsella fused to superior volsella, consisting of 2–4 small tubercles each bearing single, simple seta, longest 22–25 µm. Gonostylus 204–232 µm long, straight, narrow basally and apically, swollen medially. HR = 0.62–0.70. HV = 1.62–1.63.

Female adult and immatures. Unknown.

Distribution (Fig. 16C). Known from Rondônia and Amazonas States, in the Brazilian Amazon.

Nilothauma leccii sp. nov.

http://zoobank.org/CBFC7D88-17AB-4BF8-9CBA-2995FDAB798B

Figures 7A, B, 16B

Type material. ***Holotype*** male, slide-mounted: Brazil, São Paulo, São Sebastião, Rio das Pedras, 23°44'27"S, 45°37'12"W, 28.x.2005, light trap, A.R. Calor et al. leg. (UFSC).

Etymology. The specific epithet is a noun in the genitive case honouring Lucas Silveira Lecci, for his friendship and prolific fieldwork.

Diagnostic characters. The male can be separated from its congeners by its large size combined with unmarked wing; spatulate anal point; superior volsella leaf-shapped; inferior volsella with strong, split setae and digitiform and strongly setose gonostylus.

Description. Male imago (n = 1). Total length 4.35 mm. Wing length 1.96 mm. Total length/wing length 2.22. Wing length/length of profemur 2.45.

Colouration. Thorax and legs brown, abdomen light brown. Wing membrane without dark markings.

Antenna. AR = 0.16. Thirteenth flagellomere 124 µm long.

Head. Temporal setae 6 in single row. Clypeus with 15 setae. Tentorium 113 µm long, maximum width 25 µm. Stipes not measurable. Palp segment lengths (in µm): 37, 33, 74, 107, 138. Third palpomere with 2 sensilla clavata subapically, longest about 25 µm long. Fifth palpomere/third palpomere 1.86.

Thorax. Antepronotum with 4 setae. Dorsocentrals 17 partly biserial posterior, acrostichals 14, prealars 6. Scutellum with 13 setae.

Wing. VR = 1.53. Brachiolum with 2 setae, R with 15 setae, R_1 with 24 setae, R_{4+5} with 31 setae, remaining veins bare.

Legs. Spur of fore tibia 65 µm long including 41 µm long scale. Mid-tibia with 1 spur, 47 µm long; hind tibia with 2 spurs, 43 and 65 µm long. Combs of mid-tibia 29 µm long, of hind tibia 47 µm long. Width at apex of fore tibia 69 µm, of mid-tibia 73 µm, of hind tibia 89 µm. Lengths and proportions of legs as in Table 6.

Hypopygium (Fig. 7A, B). Tergite IX without dorsal lobes, posterior margin subtriangular with 7 setae to each side of the anal point. Anal point spatulate, 59 µm long, 10 µm wide basally, 17 µm wide medially. Tergite bands not continuous. Laterosternite IX with 4 setae. Phallapodeme 61 µm long; transverse sternapodeme 35 µm long. Gonocoxite 171 µm long. Inferior volsella weakly curved, 113 µm long, 15 µm wide subapically, with microtrichia and 7 strong, apically split setae. Superior volsella leaf-shaped, 69 µm long, 10 µm wide at base, 23 µm wide medially, covered with

Table 6. Lengths (in µm) and proportions of leg segments in *Nilothauma leccii* sp. nov., adult male (n = 1).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**	**ta$_3$**	**ta$_4$**
p_1	801	670	972	490	384	286
p_2	874	605	400	180	139	90
p_3	964	989	596	302	261	155
	ta$_5$	**LR**	**BV**	**SV**	**BR**	
p_1	139	1.45	1.88	1.51	1.7	
p_2	65	0.66	3.97	3.69	4.3	
p_3	98	0.60	3.09	3.27	4.8	

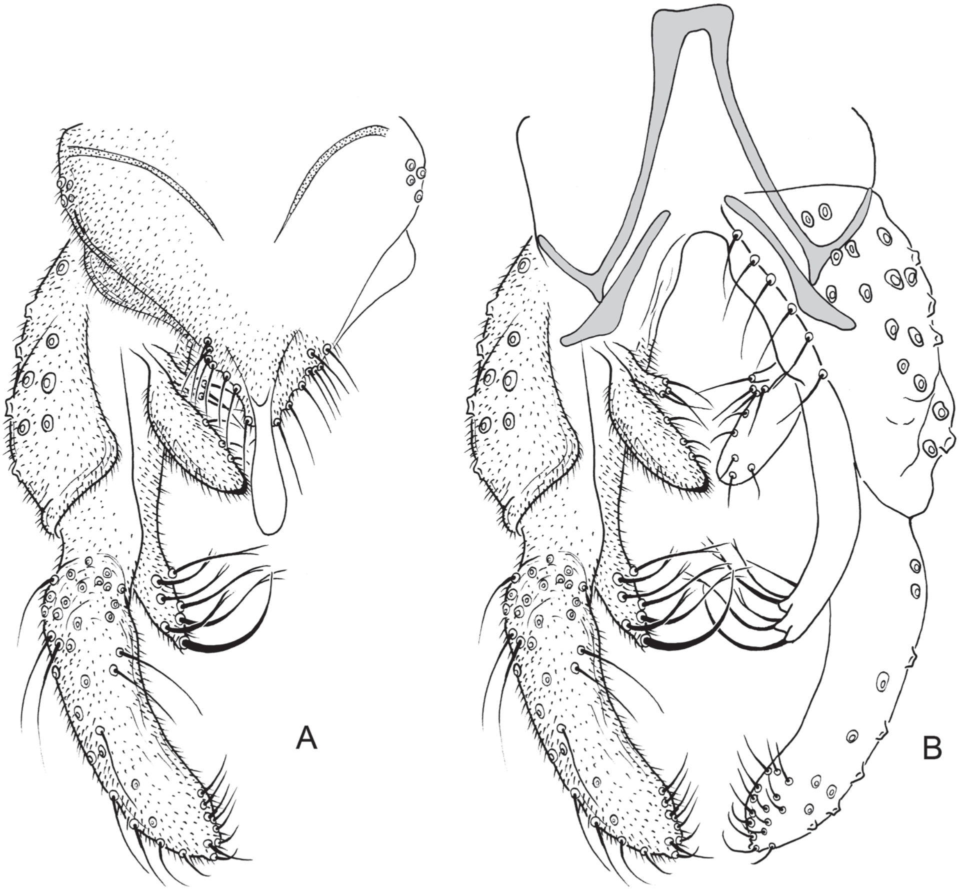

Figure 7. *Nilothauma leccii* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

microtrichia and with few weak setae ventrally and along inner margin. Median volsella narrow, 48 µm long, covered with microtrichia and with 4 setae on tubercles at apex, setae about 23 µm long. Gonostylus digitiform, strongly setose, 163 µm long, 37 µm wide medially. HR = 1.05. HV = 2.67.

Female adult and immatures. Unknown.

Distribution (Fig. 16B). Only known from São Paulo State in Brazil.

Nilothauma marianoi sp. nov.

http://zoobank.org/2F9585A3-AE43-47C7-BD91-C4EE9B23EEBC

Figures 8A, B, 16B

Type material. ***Holotype*** male, slide-mounted: Brazil, Bahia, Barreiras, Rio de Janeiro, cachoeira Acaba Vidas, 11°53'40"S, 45°36'57"W, 722 m a.s.l., 14.x.2008, light trap, A.R. Calor, R. Mariano & S. Mateus leg. (UFSC).

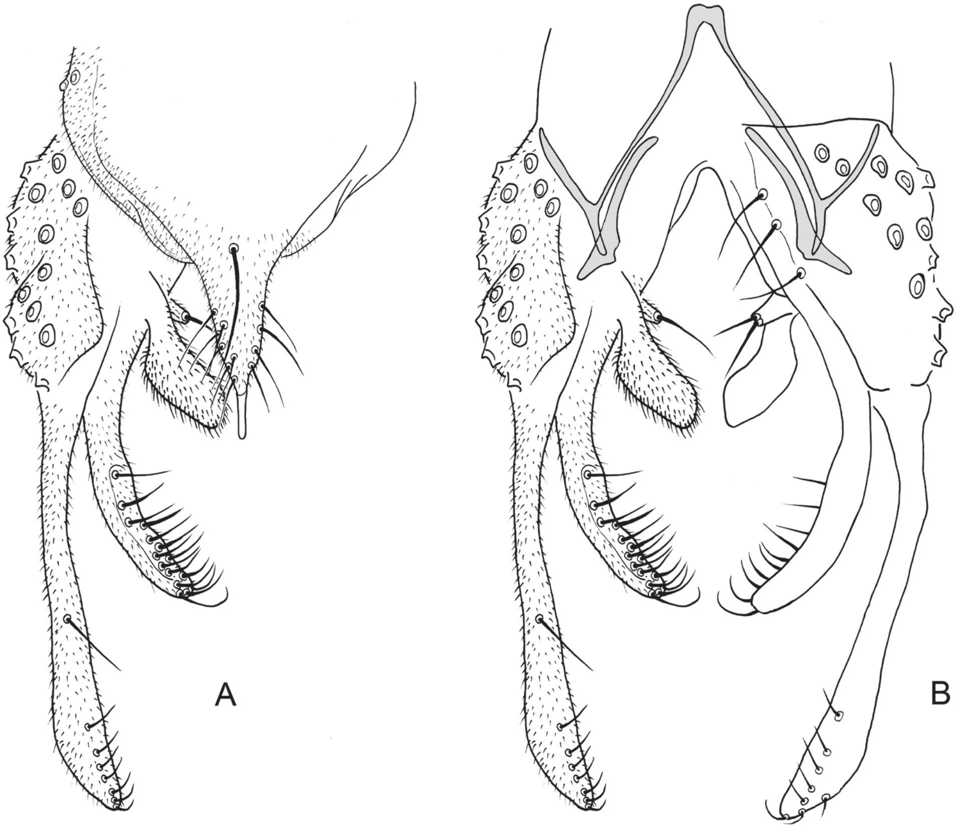

Figure 8. *Nilothauma marianoi* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Etymology. The specific epithet is a noun in the genitive case honouring Rodolfo Mariano, for his friendship and prolific fieldwork.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: wing without dark markings; tergite IX without setose dorsal lobe(s) or thorns, with single, strong median seta, with narrowly triangular posterior margin and small, apical, parallel-sided anal point.

Description. Male imago (n = 1). Total length 3.51 mm. Wing length 1.45 mm. Total length/wing length 2.43. Wing length/length of profemur 2.27.

Colouration. Thorax and legs brown, abdomen light brown. Wing membrane without dark markings.

Antenna. AR = 0.19. Thirteenth flagellomere 152 μm long.

Head. Temporal setae 6 in partly double row. Clypeus with 9 setae. Tentorium 98 μm long, maximum width 18 μm. Stipes not measurable. Palp segment lengths (in μm): 17, 18, 44, 99, 117. Sensilla clavata on third palpomere not discernable. Fifth palpomere/third palpomere 2.66.

Thorax. Dorsocentrals 6 in single row, acrostichals 4, prealars 2. Scutellum with 2 setae.

Table 7. Lengths (in µm) and proportions of leg segments in *Nilothauma marianoi* sp. nov., adult male (n = 1).

	Fe	**Ti**	**ta_1**	**ta_2**	**ta_3**	**ta_4**
p_1	637	458	645	401	310	221
p_2	621	425	261	131	90	65
p_3	694	686	384	180	180	114
	ta_5	**LR**	**BV**	**SV**	**BR**	
p_1	106	1.41	1.68	1.70	2.6	
p_2	49	0.62	3.90	4.05	5.0	
p_3	74	0.55	3.22	3.60	7.1	

Wing. VR = 1.39. Brachiolum with 1 seta, R with 8 setae, R_{4+5} with 1 apical seta, remaining veins bare.

Legs. Spur of fore tibia 68 µm long including 28 µm long scale. Mid-tibia with 1 spur, 47 µm long; hind tibia with 2 spurs, 43 and 61 µm long. Combs of mid-tibia 21 µm long, of hind tibia 26 µm long. Width at apex of fore tibia 47 µm, of mid-tibia 48 µm, of hind tibia 52 µm. Lengths and proportions of legs as in Table 7.

Hypopygium (Fig. 8A, B). Tergite IX without dorsal lobes, with single, median, strong setae, posterior margin narrowly subtriangular with 7 setae to each side. Anal point situated apically, small, parallel-sided with rounded apex, 14 µm long, 4 µm wide basally, 3 µm wide medially. Tergite bands lacking. Laterosternite IX with 2 setae. Phallapodeme 51 µm long; transverse sternapodeme 11 µm long. Gonocoxite 104 µm long. Inferior volsella weakly curved, 103 µm long, 11 µm wide subapically, with microtrichia and 18 setae in apical one-half. Superior volsella subquadrangular, 48 µm long, 17 µm wide medially, covered with microtrichia. Median volsella consisting of 14 µm long tubercle, covered with microtrichia and with 1 strong apical seta, setae about 19 µm long. Gonostylus nearly straight, 104 µm long, 10 µm wide medially, 17 µm wide subapically. HR = 0.72. HV = 2.44.

Female adult and immatures. Unknown.

Distribution (Fig. 16B). Only known from Bahia State in Brazil.

Nilothauma mateusi **sp. nov.**

http://zoobank.org/679EA037-9083-4F6D-9460-3F9F8E590EA2

Figures 9A, B; 16B

Type material. ***Holotype*** male, slide-mounted: Brazil, Mato Grosso, Nova Xavantina, Fazenda Sr. Queté, Córrego Cachoeira, 14°32.817'S, 52°31.395'W, 16.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg. (UFSC).

Etymology. The specific epithet is a noun in the genitive case honouring Sidnei Mateus, for his friendship and prolific fieldwork.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: wing without markings; tergite IX with pair of rounded lobes submedially with about 14 long setae; anal point parallel-sided; superior volsella small, subtriangular, projecting medially, with 2 setae on tubercles apically.

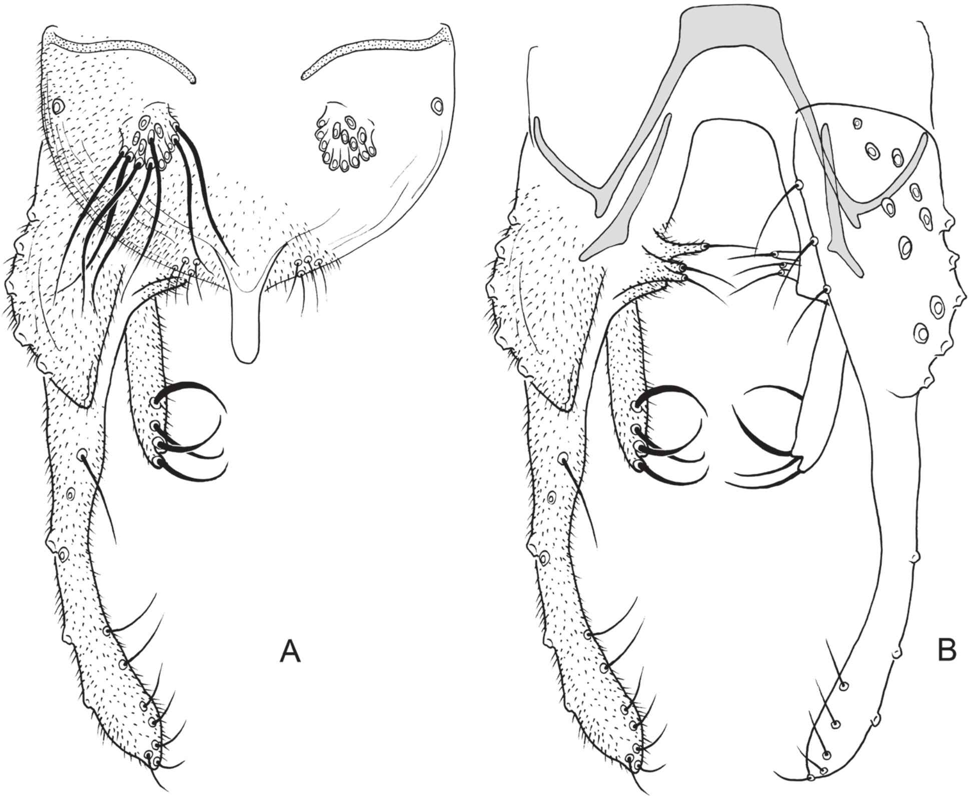

Figure 9. *Nilothauma mateusi* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Description. Male imago (n = 1). Total length 2.09 mm. Wing length 0.87 mm. Total length/wing length 2.40. Wing length/length of profemur 2.41.

Colouration. Thorax and legs brown, abdomen light brown. Wing membrane without dark markings.

Antenna. AR = 0.19. Thirteenth flagellomere 82 μm long.

Head. Temporal setae 7 in single row. Clypeus with 9 setae. Tentorium 55 μm long, maximum width 12 μm. Stipes not measurable. Palp segment I–III lengths (in μm): 21, 19, 55; remaining palp segments lost. Third palpomere with 2 sensilla clavata subapically, longest about 10 μm.

Thorax. Dorsocentrals 8 in single row, acrostichals 6, prealars 2. Scutellum with 2 setae.

Wing. VR = 1.64. Brachiolum with 1 seta, R with 6 setae, R_1 with 2 setae, R_{4+5} with 4 setae, remaining veins bare.

Legs. Spur of fore tibia 37 μm long including 18 μm long scale. Mid-tibia with 1 spur, 23 μm long; hind tibia with 2 spurs, 19 and 28 μm long. Combs of mid-tibia 14 μm long, of hind tibia 17 μm long. Width at apex of fore tibia 29 μm, of mid-tibia 30 μm, of hind tibia 33 μm. Lengths and proportions of legs as in Table 8.

Table 8. Lengths (in µm) and proportions of leg segments in *Nilothauma mateusi* sp. nov., adult male (n = 1).

	Fe	Ti	ta_1	ta_2	ta_3	ta_4
p_1	360	272	340	136	112	68
p_2	352	248	140	64	52	32
p_3	416	392	208	108	112	72
	ta_5	LR	BV	SV	BR	
p_1	40	1.25	2.73	1.86	2.0	
p_2	24	0.56	4.30	4.29	2.8	
p_3	40	0.53	3.06	3.88	4.6	

Hypopygium (Fig. 9A, B). Tergite IX with 4 weak setae to each side of the anal point and pair of rounded lobes submedially, each with about 14 long setae, longest about 50 µm long. Anal point parallel-sided with rounded apex, 23 µm long, 12 µm wide basally, 8 µm wide medially. Tergite bands not continuous. Laterosternite IX with 1 seta. Phallapodeme 35 µm long; transverse sternapodeme 19 µm long. Gonocoxite 73 µm long. Inferior volsella straight, 43 µm long, 7 µm wide subapically, with microtrichia and 4 strong apical setae. Superior volsella projecting medially, subtriangular with two apical tubercles, 14 µm long, 7 µm wide at base, 4 µm wide subapically, covered with microtrichia and with 2 apical setae, longest 9 µm long. Median volsella consisting of single strong tubercle, about 12 µm long, with single 10 µm long setae at apex. Gonostylus curved, 101 µm long, 10 µm wide medially, 14 µm wide subapically. HR = 0.72. HV = 2.07.

Female adult and immatures. Unknown.

Distribution (Fig. 16B). Only known from Mato Grosso State in Brazil.

Nilothauma maya sp. nov.

http://zoobank.org/0165F284-D9E4-4FF1-B207-C4EE505A0E00

Figures 10A, B, 16B

Type material. ***Holotype*** male, slide-mounted: Mexico, Campeche, Calacmul, Ejido Nuevo Becan, El Chorro, 18°35'26"N, 89°15'29"W, 130 m a.s.l., 30.iv.1997, light trap, A. Contreras-Ramos et al. leg. (ZMBN).

Etymology. Named after the Maya people, who used to live in the area. The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: pale brown species; wing without markings; tergite IX without setose dorsal lobe(s) or spine; anal point spatulate; superior volsella slender, curved, tapering; gonostylus curved, with strong setae on protruberance on inner margin in basal one-third.

Description. Male imago (n = 1). Total length 2.43 mm. Wing length 1.12 mm. Total length/wing length 2.17. Wing length/length of profemur 2.15.

Colouration. Pale brown. Wing membrane without dark markings.

Antenna. AR = 0.18. Thirteenth flagellomere 112 µm long.

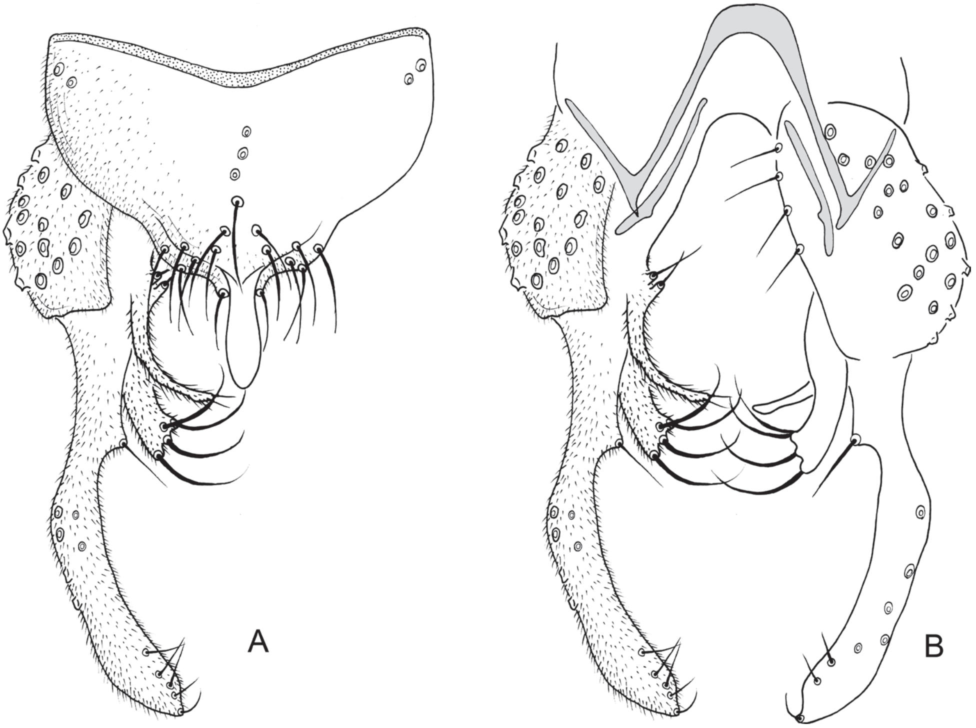

Figure 10. *Nilothauma maya* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Head. Temporal setae 4 in single row. Clypeus with 13 setae. Tentorium and stipes not measurable. Palp segment lengths (in µm): 21, 28, 65, 117, 144. Third palpomere with 2 sensilla clavata subapically, longest 19 µm long. Fifth palpomere/third palpomere 2.22.

Thorax. Dorsocentrals 8 in single row, acrostichals 8, prealars 2. Scutellum with 2 setae.

Wing. VR = 1.44. Brachiolum with 1 seta, R with 10 setae, R_1 with 12 setae, R_{4+5} with 15 setae, remaining veins bare.

Legs. Spur of fore tibia 48 µm long including 21 µm long scale. Mid-tibia with 1 spur, 26 µm long; hind tibia with 2 spurs, 25 and 33 µm long. Combs of mid-tibia 12 µm long, of hind tibia 17 µm long. Width at apex of fore tibia 36 µm, of mid-tibia 40 µm, of hind tibia 44 µm. Lengths and proportions of legs as in Table 9.

Hypopygium (Fig. 10A, B). Tergite IX without lobes, with 8 setae above anal point and 5 somewhat weaker setae to each side of anal point. Anal point spatulate, 36 µm long, maximum width 11 µm. Tergite bands continuous. Laterosternite IX with 2 setae. Phallapodeme 48 µm long; transverse sternapodeme 27 µm long. Gonocoxite 104 µm long. Inferior volsella curved, 55 µm long, 14 µm wide subapically, with microtrichia and 4 strong apical setae. Superior volsella slender, curved, tapering, 54 µm

Table 9. Lengths (in µm) and proportions of leg segments in *Nilothauma maya* sp. nov., adult male (n = 1).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**	**ta$_3$**	**ta$_4$**
p_1	520	372	–	–	–	–
p_2	484	308	208	76	56	32
p_3	504	484	232	132	140	88
	ta$_5$	**LR**	**BV**	**SV**	**BR**	
p_1	–	–	–	–	–	
p_2	28	0.68	5.21	3.81	3.4	
p_3	48	0.48	2.99	4.26	4.7	

long, 11 µm wide at base, 3 µm wide subapically, covered with microtrichia and with 2 weak apical setae. Median volsella consisting of two small tubercles, about 4 µm long, each with single setae at apex, longest 15 µm long. Gonostylus 131 µm long, curved, with single, strong setae on protuberance on inner margin at 27 µm from base, setae 21 mm long. HR = 0.79. HV = 1.85.

Female adult and immatures. Unknown.

Remarks. The slide is distorted and the drawings are composites of left and right side.

Distribution (Fig. 16B). Only known from Campeche State in Mexico.

Nilothauma reissi (Soponis, 1987)

Figure 17C

Additional material. 1 male, slide-mounted: Brazil, Santa Catarina, São Francisco do Sul, Distrito do Saí, 26°13'40"S, 48°40'50"W, CEPA Vila da Glória, 11–15.xi.2019, #143, light trap, L.C. Pinho et al. leg. 1 male, slide-mounted: Brazil, São Paulo, Santa de Rosa Viterbo, bridge at Tio Zito, 27.ix. 2000, light trap, H.F. Mendes & T. Andersen leg. 1 male, slide-mounted: Brazil, Mato Grosso, Ribeirão Cascalheira, Estrada Fazenda Manaus, 1° af. Rio Bonito, 12°57.088'S, 51°52.480'W, 08.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg.

Distribution (Fig. 17C). The species was described from the Amazonas by Soponis (1987) and was later recorded from Minas Gerais and São Paulo States in northern and south-eastern Brazil by Mendes and Andersen (2009). The range is now extended to Mato Grosso and Santa Catarina States.

Nilothauma soka Andersen, Bello-González & Hagenlund, 2016

Figure 17C

Additional material. 2 males, slide-mounted: Brazil, Rondônia, Candeias do Jamari, Rio Preto, Ponte de Madeira, #01, 08°52'40"S, 63°38'02"W, 19–20.vii.2012, light trap, R. Boldrini & A.S. Fernandes leg. 2 males, slide-mounted: Brazil, Roraima, Boa Vista, Rio Cauamé, 02°52'06"N, 60°44'24"W, 9.iii.2009, light trap, L.M. Fusari leg. 2 males, slide-mounted: Brazil, Amazonas, Barcelos, Rio Aracá, #9, 69 m a.s.l., 00°24'39"N, 63°23'12"W, 28.vii–06.viii.2009, light trap #3, N. Hamada et al. leg. 3 males, slide-mouted: Brazil, Amazonas, Barcelos, Rio Aracá, Foz do Igarapé Cuieiras, 00°19'15"N, 63°16'15"W, 35 m a.s.l., 30.vii–01.viii.2009, light trap #11, N. Hamada et al. leg.

Distribution (Fig. 17C). The species was originally described from the Amazonas State by Andersen et al. (2016); the range is now extended to the Rondônia and Roraima States in the Brazilian Amazon.

Nilothauma strebulosum **(Adam & Sæther, 2000)**

Figure 16D

Additional material. 1 male, slide-mounted: Brazil, Mato Grosso, Nova Xavantina, Fazenda Sr. Queté, Córrego Voadeira, 14°32.187'S, 52°30.902'W, 16.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg.

Distribution (Fig. 16D). The species was originally described from Costa Rica by Adam and Sæther (2000); the range is now extended to Mato Grosso State, central Brazil.

Nilothauma terena **sp. nov.**

http://zoobank.org/140D5884-DBE1-403A-AD55-6AD631840573

Figures 11A, B, 12A–H, 16A

Type material. ***Holotype*** male with larval and pupal exuvia, slide-mounted: Brazil, São Paulo, São Carlos, Campus UFSCar, Córrego do Fazzari, 21°59'S, 47°54'W, 11.ix.2008, L.C. Pinho & F.L. Silva leg. (UFSC).

Etymology. The specific epithet honours the Terena indigenous people from São Paulo State (Brazil). The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by having tergite IX with broadly rounded posterior margin without anal point, with anterolateral thorns, with dorsolateral lobes with few, strong setae and posteriolateral, narrowly subtriangular projection. The pupa can be recognised by having long, taeniate frontal setae and sternite I with extensive shagreen. The larva can be recognised by apparently having antenna with five segments only and by having mentum and inner teeth of mandible somewhat darker pigmented.

Description. Male imago (n = 1). Total length 2.67 mm. Wing length 1.21 mm. Total length/wing length 2.21. Wing length/length of profemur 2.11.

Colouration. Thorax and legs brown, abdomen light brown. Wing membrane without dark markings.

Antenna. AR = 0.21. Thirteenth flagellomere 120 μm long.

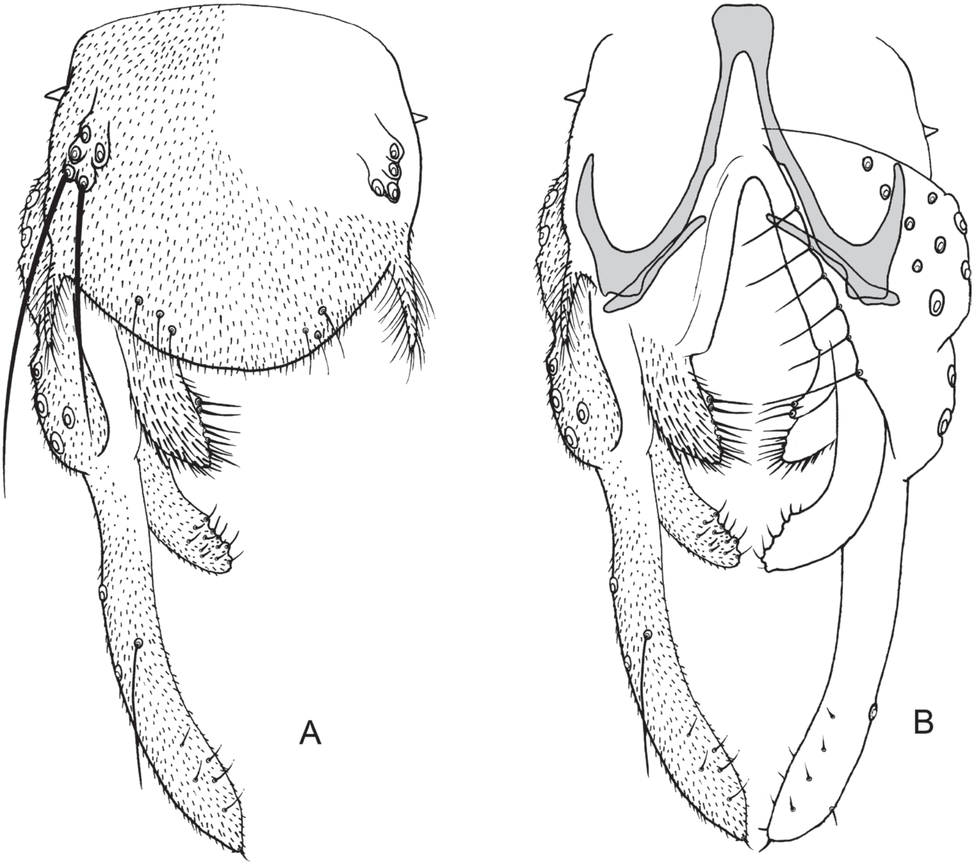

Figure 11. *Nilothauma terena* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with d tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Head. Temporal setae 5 in single row. Clypeus with 13 setae. Tentorium 62 µm long, maximum width 15 µm. Stipes not measurable. Palp segment lengths (in µm): 20, 23, 57, 92, 106. Third palpomere with 2 sensilla clavata subapically, longest about 25 µm. Fifth palpomere/third palpomere 1.87.

Thorax. Dorsocentrals 5 in single row, acrostichals 4, prealars 2. Scutellum with 2 setae.

Wing. VR = 1.46. Brachiolum with 1 seta, R with 6 setae, R_1 with 1 seta, R_{4+5} with 1 apical seta, remaining veins bare.

Legs. Spur of fore tibia 62 µm long including 32 µm long scale. Mid-leg missing; hind tibia with 2 spurs, 28 and 46 µm long. Combs of hind tibia 18 µm long. Width at apex of fore tibia 37 µm, of hind tibia 39 µm. Lengths and proportions of legs as in Table 10.

Hypopygium (Fig. 11A, B). Tergite IX with rounded posterior margin with altogether 6 marginal setae in two posteriolateral groups; with dorsolateral lobes with

Table 10. Lengths (in µm) and proportions of leg segments in *Nilothauma terena* sp. nov., adult male (n = 1).

	Fe	Ti	ta_1	ta_2	ta_3	ta_4
p_1	572	359	–	–	–	–
p_2	–	–	–	–	–	–
p_3	563	574	310	155	147	90
	ta_5	**LR**	**BV**	**SV**	**BR**	
p_1	–	–	–	–	–	
p_2	–	–	–	–	–	
p_3	49	0.57	3.22	3.58	7.1	

5 strong setae, longest setae 65 µm long; with posteriolateral, narrowly subtriangular projections, 14 µm long, 6 µm wide at base. Tergite band not apparent. Laterosternite IX without setae; with small anteriolateral thorn. Phallapodeme 33 µm long; transverse sternapodeme 11 µm long. Gonocoxite 83 µm long. Inferior volsella digitiform, curved, 55 µm long, 11 µm wide medially, with microtrichia and 12 short setae subapically. Superior volsella 29 µm long, 12 µm wide at base, 13 µm wide medially, covered with microtrichia and with marginal setae. Median volsella subtriangular with 2 apical setae on small tubercles, setae about 6 µm long. Gonostylus weakly curved, 97 µm long, 14 µm wide medially. HR = 0.85. HV = 2.75.

Female adult. Unknown.

Pupa (n = 1). Total length 3.59 mm. Exuviae pale brown.

Cephalothorax (Fig. 12A, B). Frontal apotome (Fig. 12A) with few wrinkles, frontal setae taeniate, 154 µm long. Thoracic horn not discernible; basal ring oval, 13 µm in diameter. Scutum with field of few weak tubercles. Antepronotals 2; precorneals 2; dorsocentrals 4, Dc1 39 µm in front of Dc2, Dc2 96 µm in front of Dc3, Dc3 23 µm in front of Dc4.

Abdomen (Fig. 12C–E). Tergite I bare; tergites II–VI with transverse anterior band of somewhat stronger spinules, merging with median field of finer shagreen; anterior band of shagreen on tergite VI separated from posterior shagreen patch; tergite VII with anterior and posterior shagreen patches; tergite VIII with anterior shagreen patch connected with narrow posterior field of finer shagreen; tergite IX bare. Sternite I (Fig. 12D) with extensive shagreen; sternite II–VII bare; sternite VIII with narrow, longitudinal field of fine shagreen. Tergite II with 159 µm long row of 36 hooks, each hook about 8 µm long. Conjunctives III/IV and IV/V with spinules extending on to preceding segment. Pedes spurii B weakly developed on segment II. Anal comb 51 µm long, consisting of 3 spurs.

Abdominal setation. Lateral setae on segments I–VIII as: 0, 3, 3, 3, 4, 4, 4, 4; posterior lateral seta on tergite IV and all lateral setae on tergites V–VIII taeniate, remaining setae hair-like. All tergites with 1 pair of O setae.

Anal lobe. As long as broad, with 1 taeniate dorsal setae and complete fringe of 19 taeniae on each side, longest 170 µm. Male genital sac over-reaches anal lobe by 119 µm.

Fourth instar larva (n = 1). Head capsule 228 µm long. Postmentum 145 µm long.

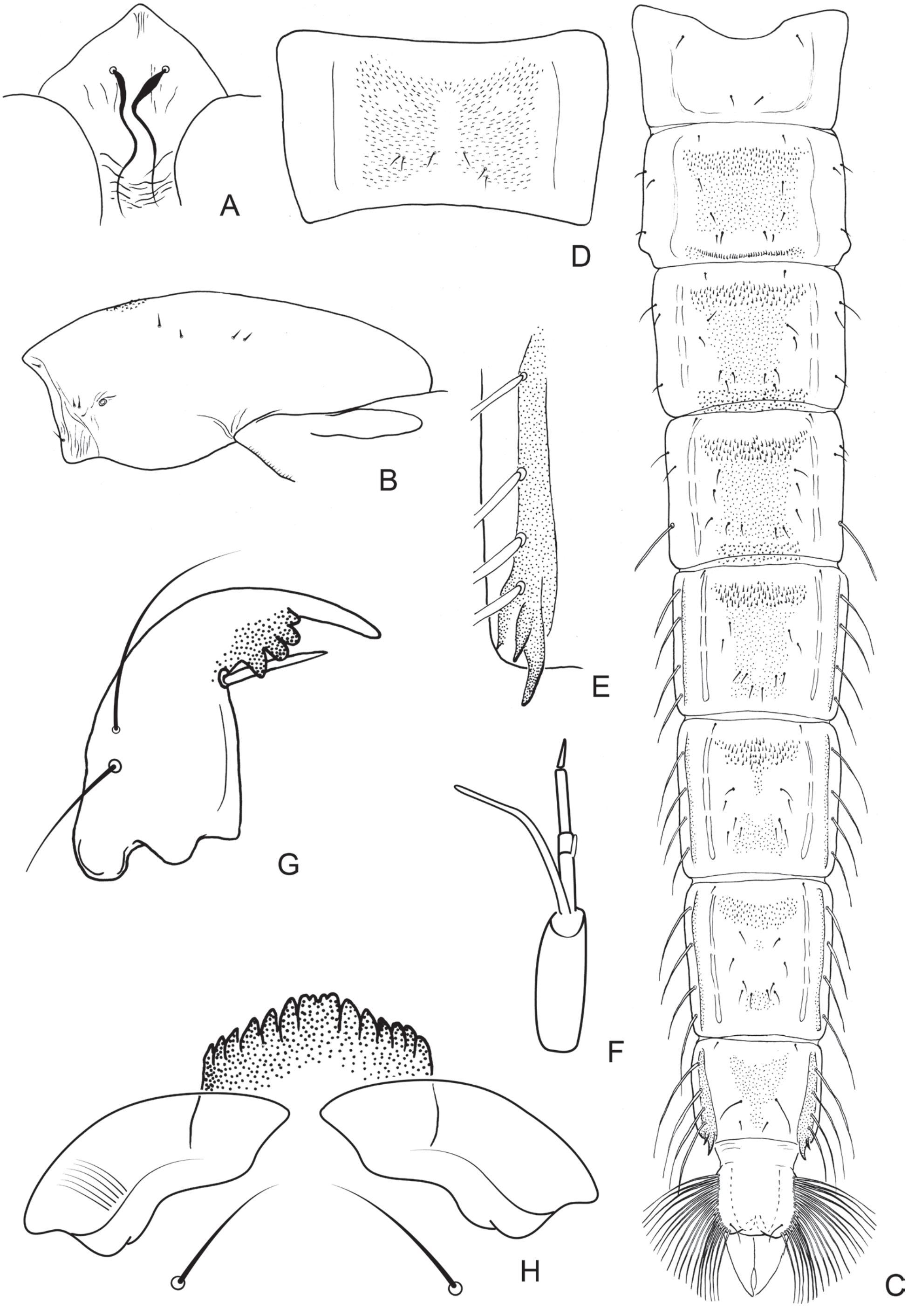

Figure 12. *Nilothauma terena* sp. nov. pupa (**A–E**) and larva (**F–H**) **A** frontal apotome **B** thorax **C** abdomen, dorsal view **D** sternite I **E** paratergite VIII **F** antenna **G** mandible **H** mentum and ventromental plates.

Head. Antenna (Fig. 12F) apparently with five segments only, length of antennal segments (in µm): 19, 10, 4, 11, 6. AR = 0.61. Basal antennal segment 10 µm wide; blade 32 µm long; accessory blade about 5 µm long. Premandible not measurable, teeth not discernible. Mandible (Fig. 12G) 69 µm long, seta subdentalis 19 µm long, inner teeth somewhat darker pigmented. Mentum (Fig. 12H) somewhat darker pigmented, 41 µm wide; middle part 10 µm wide with 2 minute inner teeth and pair of slightly larger lateral teeth; with 6 pairs of pointed, medially curved lateral teeth. Ventromental plates 98 µm wide, medially separated by 10 µm. Seta submenti 46 µm long.

Abdomen. Lost.

Distribution (Fig. 16A). Known from São Paulo State, south-eastern Brazil.

Nilothauma txukuyana sp. nov.

http://zoobank.org/8D8DBE02-E551-48F2-AFD8-DFF0B4263FCE

Figures 13A, B, 16B

Type material. ***Holotype*** male, slide-mounted: Brazil, Pará, Rio Paru do Oeste, Malloca Apicó, 20.iv.1962, at light, E.J. Fittkau leg. (A 366-1, ZSM). ***Paratypes*:** 15 males, same data as holotype (ZSM, ZMBN, UFSC).

Etymology. The specific epithet honours the Txukuyana, indigenous people from Amazonas and Pará States in Brazil and from Suriname. The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by having tergite IX with broadly-rounded posterior margin without anal point, with dorsolateral lobes with few, strong setae and posteriolateral, strongly setose, subtriangular projection.

Description. Male imago (n = 5–8). Total length 2.17–2.44, 2.25 mm. Wing length 1.00–1.09, 1.05 mm. Total length/wing length 2.02–2.33, 2.16. Wing length/length of profemur 2.16–2.26, 2.21.

Colouration. Head, thorax and legs brown; abdomen light brown. Wing membrane without dark markings.

Antenna. AR = 0.26–0.29, 0.28. Thirteenth flagellomere 132–156, 145 µm long.

Head. Temporal setae 6–10, 7 in single row. Clypeus with 13–16, 15 setae. Tentorium 69–83, 77 µm long, maximum width 14–19, 19 µm. Stipes not measurable. Palp segment lengths (in µm): 18–25, 21; 23–28, 26; 56–60, 57; 76–81, 79; 102–115, 107. Third palpomere with 2 sensilla clavata subapically, longest about 15 µm long. Fifth palpomere/third palpomere 1.72–1.98, 1.85.

Thorax. Dorsocentrals 4–7, 6 in single row, acrostichals apparently 4–6, 5 anterior, prealars 1–2, 2. Scutellum with 2 setae.

Wing. VR = 1.44–1.54, 1.50. Brachiolum with 1 seta, R with 7–9, 8 setae, R_1 with 5–8, 7 setae, R_{4+5} with 9–13, 11 setae apically, remaining veins bare.

Legs. Spur of fore tibia 48–54, 52 µm long including 20–25, 22 µm long scale. Mid-tibia with 1 spur, 29–35, 32 µm long; hind tibia with 2 spurs, 22–28, 25 and

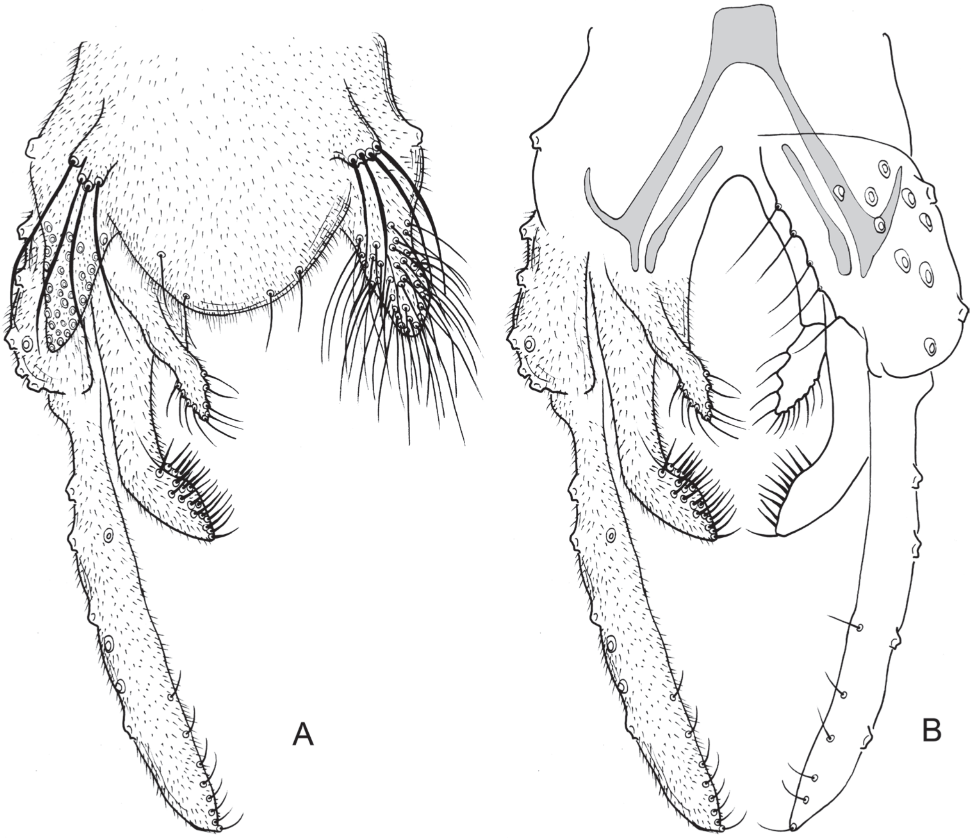

Figure 13. *Nilothauma txukuyana* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

33–39, 36 µm long. Combs of mid-tibia 17–18, 18 µm long, of hind tibia 19–22, 21 µm long. Width at apex of fore tibia 33–37, 35 µm, of mid-tibia 33–38, 36 µm, of hind tibia 39–41, 40 µm. Lengths and proportions of legs as in Table 11.

Hypopygium (Fig. 13A, B). Tergite IX with rounded posterior margin with 4–7, 5 marginal setae; with dorsolateral lobes with 3–4, 4 strong setae, longest setae 44–55, 50 µm long; with posteriolateral subtriangular, strongly setose projection, 35–41, 38 µm long, 22–25, 24 µm wide at base. Tergite band not apparent. Laterosternite IX with single setae. Phallapodeme 47–55, 49 µm long; transverse sternapodeme 17–19, 18 µm long. Gonocoxite 83–89, 87 µm long. Inferior volsella digitiform, curved, 62–72, 67 µm long, 11–14, 12 µm wide medially, with microtrichia and 13–17, 15 setae subapically. Superior volsella 25–29, 27 µm long, 8–11, 10 µm wide at base, 7–10, 9 µm wide medially, covered with microtrichia and with marginal setae. Median volsella small, broadly triangular, apparently without setae. Gonostylus nearly straight, 126–135, 130 µm long, 17–19, 18 µm wide medially. HR = 0.65–0.68, 0.66. HV = 1.78–1.87, 1.82.

Table 11. Length (in µm) and proportions of legs of *Nilothauma txukuyana* sp. nov., adult males (n = 5–7).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**
p_1	457–523, 482	319–359, 338	474–547, 515	194–221, 203
p_2	449–474, 462	286–310, 301	147–179, 162	65–74, 69
p_3	507–556, 529	458–482, 467	245–278, 263	114–139, 127
	ta$_3$	**ta$_4$**	**ta$_5$**	**LR**
p_1	147–163, 157	106–123, 114	57–65, 59	1.49–1.59, 1.52
p_2	41–49, 46	25–33, 29	24–32, 26	0.50–0.58, 0.54
p_3	114–147, 129	73–90, 78	41–49, 47	0.54–0.58, 0.56
	BV		**SV**	**BR**
p_1	2.47–2.54, 2.51		1.54–1.64, 1.59	2.43–3.46, 2.71
p_2	5.13–5.73, 5.45		4.36–5.06, 4.73	2.77–3.76, 3.38
p_3	3.20–3.57, 3.30		3.70–4.00, 3.79	4.33–5.00, 4.60

Female imago and immatures. Unknown.

Distribution (Fig. 16B). Known from Pará State, Brazil.

Nilothauma werekena sp. nov.

http://zoobank.org/2B7C1444-B834-4FAD-BE69-E0417DD42812

Figures 14A–C, 16D

Type material. ***Holotype*** male, slide-mounted: Brazil, Amazonas, Barcelos, Rio Aracá, Foz do Igarapé Cuieiras, #11, 00°19'15"N, 63°16'15"W, 35 m a.s.l., 30.vii–01.viii.2009, light trap, N. Hamada et al. leg. (UFSC). ***Paratypes*:** 4 males, slide-mounted, same data as holotype (INPA). 2 males, slide-mounted, same data as previous, except: #9, 00°24'39"N, 63°23'12"W, 69 m a.s.l., 28.vii–06.viii.2009, light trap #3, N. Hamada et al. leg (MZSP).

Etymology. The specific epithet honours the Werekena indigenous people from the Rio Negro Basin in the Amazon. The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX with one low, but wide median dorsal protruberance with about 30 strong setae; anal point spatulate; superior volsella covered with microtrichia, fused to median volsella; laterosternite IX with thorn.

Description. Male imago (n = 5–7, unless otherwise stated). Total length 1.89–2.26, 2.11 mm. Wing length 0.98–1.11, 1.05 mm. Total length/wing length 1.90–2.15, 1.99. Wing length/length of profemur 2.21–2.53, 2.37.

Colouration. Head, thorax, legs and abdomen uniformly brown. Wing membrane without dark markings.

Antenna. AR = 0.32–0.39, 0.35. Thirteenth flagellomere 230–274, 260 µm long.

Head. Temporal setae 7–8, 7 in single row. Clypeus with 10–14, 12 setae. Tentorium 47–75, 65 µm long, maximum width 12–20, 17 µm. Stipes 80–117, 100 (4) µm long. Palp segment lengths (in µm): 20–32, 27; 22–27, 25; 65–85, 72; 95–125, 110; 87–132, 115. Third palpomere with 2–5, 4 sensilla clavata subapically, longest 12–15, 14 µm long. Fifth palpomere/third palpomere 1.21–1.75, 1.54.

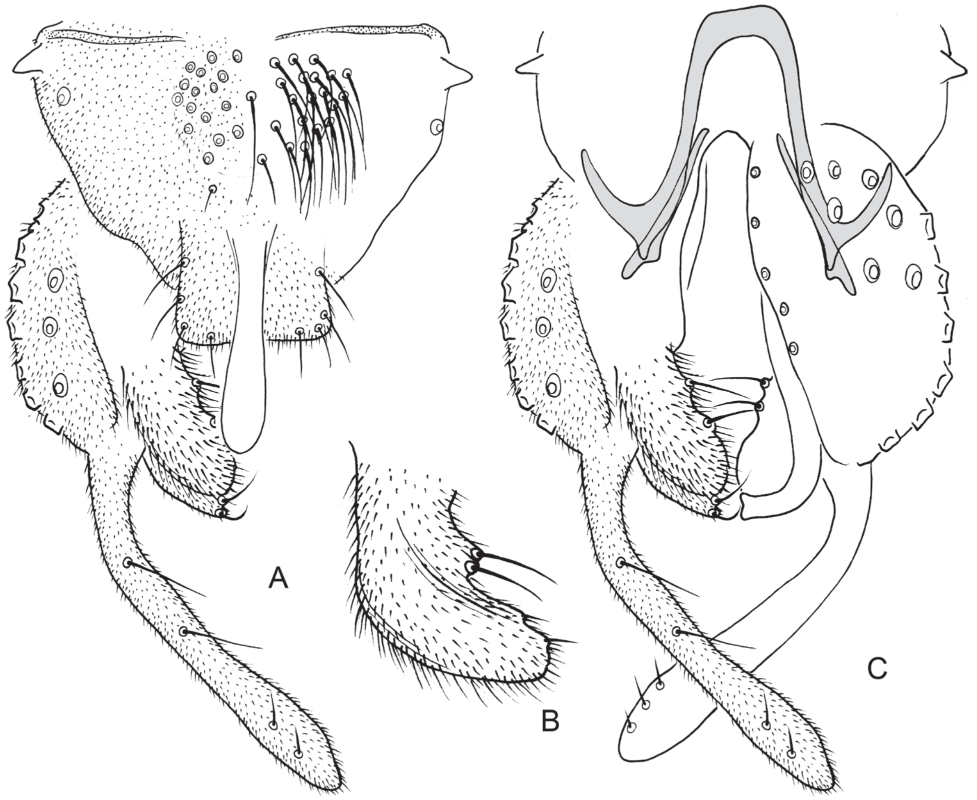

Figure 14. *Nilothauma werekena* sp. nov. adult male **A** hypopygium, dorsal view **B** superior volsella, dorsal view **C** hypopygium with anal point and tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Thorax. Dorsocentrals 6–8, 7 in single row, acrostichals 10–14, 12, prealars 2. Scutellum with 2 setae.

Wing. VR = 1.21–1.32, 1.27. Brachiolum with 1 seta, R with 11–12, 11 setae, R_1 with 5–8, 7 setae, R_{4+5} with 11–17, 15 setae, remaining veins bare.

Legs. Spur of fore tibia 39–44, 42 µm long including 15–20, 17 µm long scale. Mid-tibia with 1 spur, 20–25, 22 µm long; hind tibia with 2 spurs, 20–25, 23 and 28–31, 30 µm long. Combs of mid-tibia 17–19, 18 µm long, of hind tibia 18–21, 19 µm long. Width at apex of fore tibia 29–39, 34 µm, of mid-tibia 34–39, 37 µm, of hind tibia 34–44, 39 µm. Lengths and proportions of legs as in Table 12.

Hypopygium (Fig. 14A–C). Tergite IX without dorsal lobe(s), with low, but wide median dorsal protruberance with 29–32, 31 strong, clustered median setae; posterior margin rounded to subrectangular, with 8–11, 9 weak setae to each side of base of anal point. Anal point spatulate, 37–47, 40 µm long, maximum width 5–10, 7 µm. Tergite bands not continuous. Laterosternite IX with 1–2, 1 seta; with anterolateral thorn. Phallapodeme 40–50, 45 µm long; transverse sternapodeme 15–25, 20 µm long. Gonocoxite 62–82, 72 µm long. Inferior volsella strongly curved, 22–30, 27 µm long,

Table 12. Lengths (in µm) and proportions of leg segments in *Nilothauma werekena* sp. nov., adult males (n = 5–7, unless otherwise stated).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**
p_1	374–501, 433	315–394, 345	443–522, 473	246–286, 266
p_2	345–463, 424	296–345, 325	177–207, 197	89–99, 94
p_3	443–532, 493	463–522, 502	266–305, 286	138–158, 148
	ta$_3$	**ta$_4$**	**ta$_5$**	**LR**
p_1	187–217, 207	118–148, 138 (4)	69–89, 79 (4)	1.36–1.47, 1.40
p_2	69–79, 74	39–49, 44	30–39, 35	0.56–0.63, 0.60
p_3	128–158, 148 (4)	89–99, 94 (4)	59–69, 55 (4)	0.57–0.61, 0.59
	BV		**SV**	**BR**
p_1	1.84–2.20, 1.95		1.55–1.66, 1.60	2.0–3.3, 2.5
p_2	3.50–4.25, 3.81		3.42–4.05, 3.71	2.3–4.7, 3.3
p_3	2.70–2.89, 2.81 (4)		3.39–3.45, 3.41	5.0–7.0, 5.9

5–8, 6 µm wide medially, with microtrichia and 3 strong, simple setae apically. Superior volsella tongue-shaped to slightly pediform, 32–40, 37 µm long, 15–25, 20 µm wide at base, densely covered with microtrichia. Median volsella fused to superior volsella, consisting of 2–3, 2 small tubercles, each bearing single, long seta. Gonostylus 70–100, 90 µm long, basal half curved, distal half straight. HR = 0.63–0.96, 0.83. HV = 2.26–2.70, 2.34.

Female adult and immatures. Unknown.

Distribution (Fig. 16D). Known from Barcelos (Amazonas State), in the Brazilian Amazon.

Nilothauma yekwana sp. nov.

http://zoobank.org/2FDCF2C9-C8ED-4675-93F2-65B893098864

Figures 15A, B, 16A

Type material. ***Holotype*** male, slide-mounted: Brazil, Roraima, Boa Vista, BR-174, Igarapé Água Boa, 02°43'32"N, 60°48'43"W, 2014, N. Hamada leg (UFSC).

Etymology. The specific epithet honours the Ye'kwana, indigenous people from the Roraima State, Brazil. The name is to be regarded as a noun in apposition.

Diagnostic characters. The male can be distinguished from its congeners by the combination of: tergite IX with two setose dorsolateral lobes; anal point absent; posterior margin of tergite IX subrectangular; inferior volsella straight, tapering to apex; superior volsella curved, projecting posteriolaterally; median volsella broad, triangular, bearing 7 strong setae.

Description. Male imago (n = 1). Total length 1.77 mm. Wing length 0.91 mm. Total length/wing length 1.95. Wing length/length of profemur 2.19.

Colouration. Head, thorax, legs and abdomen uniformly light brown. Wing membrane without dark markings.

Antenna. AR = 0.22. Thirteenth flagellomere 137 µm long.

Head. Temporal setae 7 in single row. Clypeus with 15 setae. Tentorium 65 µm long, maximum width 12 µm. Stipes 80 µm long. Palp segment I–III lengths (in µm):

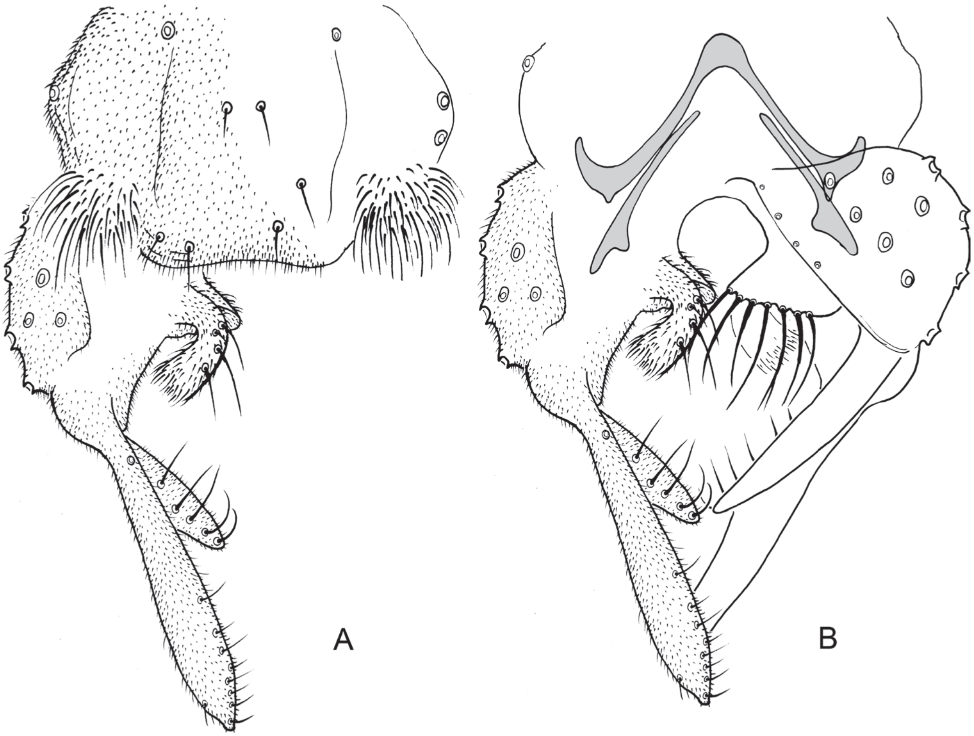

Figure 15. *Nilothauma yekwana* sp. nov. adult male **A** hypopygium, dorsal view **B** hypopygium with tergite IX removed, dorsal aspect to the left and ventral aspect to the right.

Table 13. Lengths (in µm) and proportions of leg segments in *Nilothauma yekwana* sp. nov., adult male (n = 1).

	Fe	**Ti**	**ta$_1$**	**ta$_2$**	**ta$_3$**	**ta$_4$**
p_1	414	296	–	–	–	–
p_2	394	256	177	59	39	30
p_3	443	414	217	99	99	79
	ta$_5$	**LR**	**BV**	**SV**	**BR**	
p_1	–	–	–	–	–	–
p_2	30	0.57	5.25	3.67	2.0	–
p_3	49	0.52	3.60	3.95	4.4	–

22, 17, 50; segment IV and V lost. Third palpomere with 2 sensilla clavata subapically, longest 15 µm.

Thorax. Dorsocentrals 5 in single row, acrostichals 10, prealars 2. Scutellum with 2 setae.

Wing. VR = 1.48. Brachiolum with 1 seta, R with 6 setae, R_{4+5} with 2 setae at apex, remaining veins bare.

Legs. Spur of fore tibia 44 µm long including 15 µm long scale. Mid-tibia with 1 spur, 20 µm long; hind tibia with 2 spurs, 20 and 25 µm long. Combs of mid-tibia 15 µm long, of hind tibia 18 µm long. Width at apex of fore tibia 39 µm, of mid-tibia 39 µm, of hind tibia 44 µm. Lengths and proportions of legs as in Table 13.

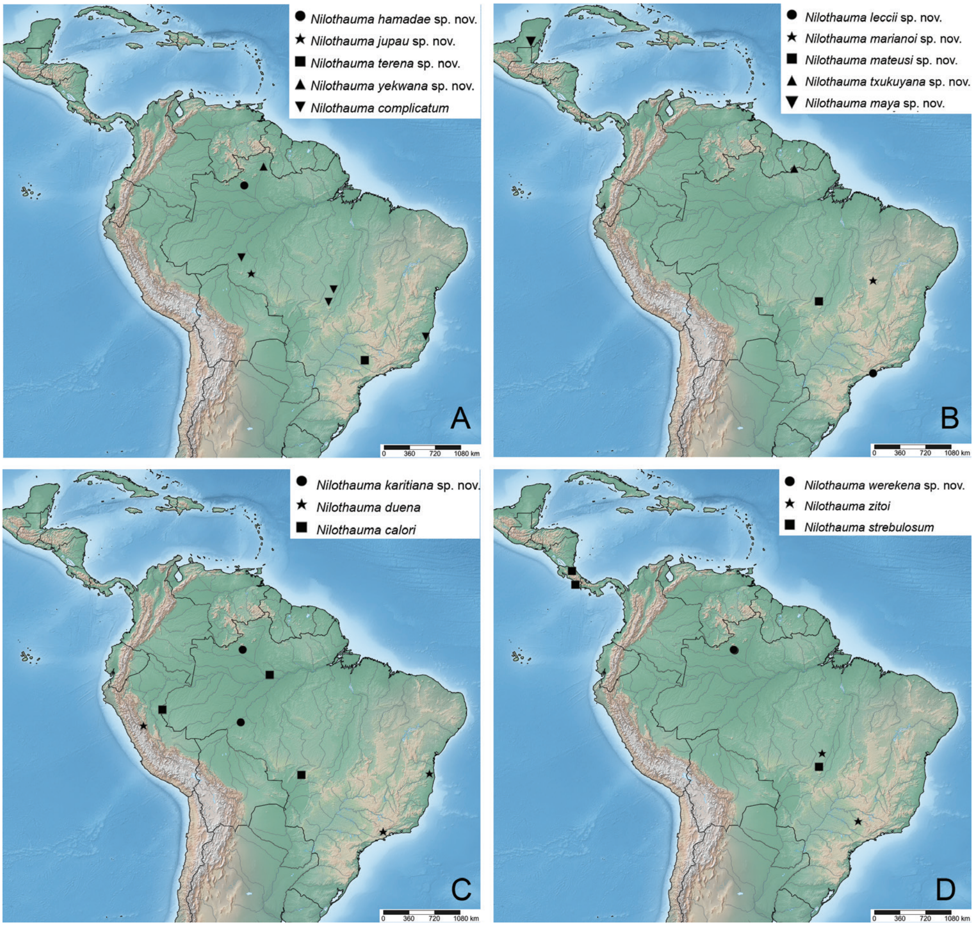

Figure 16. Distribution maps of Neotropical *Nilothauma* species **A** *N. hamadae* sp. nov., *N. jupau* sp. nov., *N. terena* sp. nov., *N. yekwana* sp. nov., *N. complicatum* Mendes & Andersen, 2009 **B** *N. leccii* sp. nov., *N. marianoi* sp. nov., *N. mateusi* sp. nov., *N. txukuyana* sp. nov., *N. maya* sp. nov. **C** *N. karitiana* sp. nov., *N. duena* Roback, 1960, *N. calori* Mendes & Andersen, 2009 **D** *N. werekena* sp. nov., *N. zitoi* Mendes & Andersen, 2009, *N. strebulosum* (Adam & Sæther, 2000).

Hypopygium (Fig. 15A, B). Tergite IX with 2 dorsolateral, densely setose lobes, setae about 15 µm long; with 2 strong setae anterolaterally, 2 medially and 4 close to posterior margin; posterior margin subquadrangular, anal point absent. Tergite bands lacking. Laterosternite IX with 1 seta. Phallapodeme 37 µm long; transverse sternapodeme 10 µm long. Gonocoxite 65 µm long. Inferior volsella straight, tapering to apex, 40 µm long, 7 µm wide medially, with microtrichia and 9 simple setae subapically. Superior volsella curved, projecting posteriolaterally, 22 µm long, 5 µm wide at base, covered with microtrichia and fringed at apex. Median volsella broad, triangular, 15 µm long, with 7 strong setae (one of them bifid), longest 20 µm. Gonostylus 75 µm long, straight. HR = 0.87. HV = 2.36.

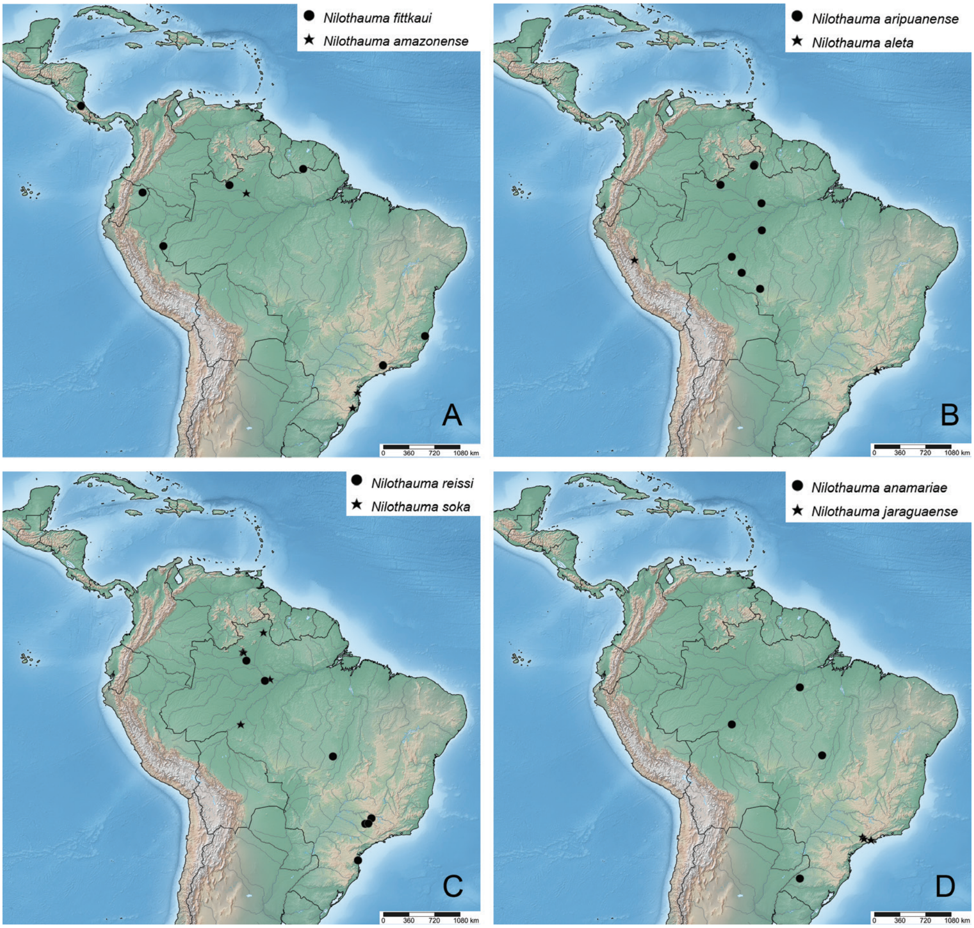

Figure 17. Distribution maps of Neotropical *Nilothauma* species **A** *N. fittkaui* (Soponis, 1987), *N. amazonense* Mendes & Andersen, 2009 **B** *N. aripuanense* Mendes & Andersen, 2009, *N aleta* Roback, 1960 **C** *N. reissi* (Soponis, 1987), *N. soka* Andersen, Bello-González & Hagenlund, 2016 **D** *N. anamariae* Dantas & Hamada, 2017, *N. jaraguaense* Mendes & Andersen, 2009.

Female adult and immatures. Unknown.

Distribution (Fig. 16A). Known from Roraima State, Brazilian Amazon.

Nilothauma zitoi Mendes & Andersen, 2009

Figure 16D

Additional material. 1 male, slide-mounted: Brazil, Mato Grosso, Ribeirão Cascalheira, Fazenda Campina Verde, Rio Suiá Miçu, 12°48.591'S, 52°06.925'W, 10.x.2007, light trap, L.C. Pinho, S. Mateus, L. Torati & F.R. Silva leg.

Distribution (Fig. 16D). The species was originally described by Mendes and Andersen (2009), based on a single male from São Paulo State; the range is now extended to the Mato Grosso State.

Key to the males of *Nilothauma* Kieffer of the world

Modified from Qi et al. (2014), Niitsuma (2016) and Andersen et al. (2016), with the inclusion of sixteen species.

1 Tergite IX without setose dorsal lobe(s) or projection(s) **2**

– Tergite IX with one to four setose dorsal lobes or projection(s) (e.g. Figs 16, 20) **19**

2 Anal point present **3**

– Anal point absent **15**

3 Tergite IX with median cluster of about 30 strong setae **4**

– Tergite IX with few, clustered setae, if numerous they are scattered (as in *N. aripuanense*) **5**

4 Superior volsella slender, without microtrichia and with lateral spine. Brazil .... ***Nilothauma jaquei* Dantas & Hamada, 2017**

– Superior volsella pediform to lingulate, covered with microtrichia and without lateral spine (Fig. 14). Brazil .... ***Nilothauma werekena* sp. nov.**

5 Wing with conspicuous dark markings (Fig. 5); abdominal tergites II, III, and VI–VIII dark brown. Brazil .... ***Nilothauma jupau* sp. nov.**

– Wing unmarked, at most with faint colour (as in *Nilothauma aleta*, best seen in dark-field filter); abdominal tergites uniformly pale to brown **6**

6 Gonostylus stout or swollen (Figs 1, 3, 6, 7) **7**

– Gonostylus slender (Fig. 10) **10**

7 Gonostylus very long, narrow basally and apically, swollen at mid-length (Fig. 6). Brazil .... ***Nilothauma karitiana* sp. nov.**

– Gonostylus stout, not distinctly swollen at mid-length (Figs 1, 3) **8**

8 Acrostichals absent; anal point wide, covering most setae along posterior margin of tergite IX (Fig. 1). Peru, Brazil .... ***Nilothauma aleta* Roback, 1960**

– Acrostichals present; anal point comparatively narrow, nearly parallel-sided, with most setae placed lateral to base of anal point **9**

9 Superior volsella tapering to apex; inferior volsella short, stout, with short, simple setae (Fig. 3). Peru, Brazil .... ***Nilothauma duena* Roback, 1960**

– Superior volsella wider at mid-length; inferior volsella long and slender, with long simple or apically split setae (Fig. 7). Brazil .... ***Nilothauma leccii* sp. nov.**

10 Superior volsella narrow, straight, curved or weakly sinuous, projecting posteriomedially, with one to six apical setae **11**

– Superior volsella wider in distal half, projecting posterio-medially or posteriolaterally, with microtrichia only **13**

11 Tergite IX with numerous scattered setae; anal point broadly lanceolate, about 20 µm wide. Brazil .... ***Nilothauma aripuanense*** **Mendes & Andersen, 2009**

– Tergite IX with one to four median setae and about 12 setae along posterior margin; anal point comparatively narrow **12**

12 Tergite IX with single seta anterior to anal point; gonostylus with two to four sub-basal dorsal setae not arising from protuberances. Brazil.................................... ....***Nilothauma paucisetis*** **Dantas & Hamada, 2017**

– Tergite IX with four aligned setae anterior to anal point; gonostylus with single sub-basal seta arising from distinct inner protuberance (Fig. 10). Neotropical Mexico... ***Nilothauma maya*** **sp. nov.**

13 Anal point parallel-sided, about 4 µm wide; inferior volsella with about 18 slender, simple setae (Fig. 8). Brazil.......................... ***Nilothauma marianoi*** **sp. nov.**

– Anal point spatulate, 15–23 µm wide; inferior volsella with few (about 3) simple, slender setae or numerous (about 12) stout, split setae apically........................ **14**

14 Superior volsella boot-shaped, projecting posterior-laterally; inferior volsella narrow, with few simple, slender setae apically. Brazil... ....***Nilothauma soka*** **Andersen, Bello-González & Hagenlund, 2016**

– Superior volsella straight, projecting posterior-medially; inferior volsella wide, with numerous stout, split setae apically. Brazil... .... ***Nilothauma anamariae*** **Dantas & Hamada, 2017**

15 Inferior volsella branched subapically. Brazil.. ....***Nilothauma complicatum*** **Mendes & Andersen, 2009**

– Inferior volsella simple **16**

16 Superior volsella pediform, without ventral transverse fold, with setae and microtrichia **17**

– Superior volsella diamond-shaped, with ventral transverse fold, with microtrichia only **18**

17 Wing vein R_1 with setae; gonostylus nearly parallel-sided in apical half. Brazil, Ecuador .... ***Nilothauma fittkaui*** **(Soponis, 1987)**

– Wing vein R_1 bare; gonostylus widest in apical one-third. Brazil .... ***Nilothauma reissi*** **(Soponis, 1987)**

18 Apex of superior volsella projecting caudad. Brazil ....***Nilothauma sooretamense*** **Mendes & Andersen, 2009**

– Apex of superior volsella projecting mesad. Brazil ....***Nilothauma involucrum*** **Mendes & Andersen, 2009**

19 Anal point lacking or rudimentary, completely covered by microtrichia **20**

– Anal point present, with microtrichia at most in basal half............................. **22**

20 Tergite IX with four lobes or projections, one anterior pair with strong, long setae and one posterio-lateral, triangular pair with weaker setae.............................. **21**

– Tergite IX with one or two dorsal lobes **27**

21 Tergite IX with posterio-lateral pair of projections short, subequal in length to anterior pair (Fig. 11); laterosternite IX with thorn. Brazil ...... ***N. terena* sp. nov.**

– Tergite IX with posterio-lateral pair of projections long, more than three times longer than anterior pair (Fig. 13); laterosternite IX without thorn. Brazil .... ***N. txukuyana* sp. nov.**

22 Dorsal projections of tergite IX differ in shape. Ghana....................................... .... ***Nilothauma insolitum* Adam & Sæther, 1999**

– Dorsal projections of tergite IX of the same shape **23**

23 Median volsella fused to superior volsella; superior volsella broadly pediform. Brazil .... ***Nilothauma fazzariense* Mendes & Andersen, 2009**

– Median volsella distinct and separated from superior volsella; superior volsella digitate, curved, with or without lateral spine **24**

24 Dorso-lateral projections of tergite IX overreaching posterior margin of tergite. Brazil .... ***Nilothauma roquei* Mendes & Andersen, 2009**

– Dorso-lateral projections of tergite IX not extended beyond posterior margin of tergite **25**

25 Superior volsella with lateral spine; laterosternite IX with thorn; posterior margin of tergite IX broadly rounded. Brazil.. .... ***Nilothauma calori* Mendes & Andersen, 2009**

– Superior volsella without lateral spine; laterosternite IX without thorn; posterior margin of tergite IX subrectangular **26**

26 Median volsella consisting of single, small tubercle bearing one seta; inferior volsella curved, not tapering to apex. Brazil, Costa Rica... .... ***Nilothauma strebulosum* (Adam & Sæther, 2000)**

– Median volsella broad, triangular, bearing 7 strong setae; inferior volsella straight, tapering to apex (Fig. 15). Brazil .... ***Nilothauma yekwana* sp. nov.**

27 Tergite IX with single, median setose dorsal lobe... **28**

– Tergite IX with two setose dorsal lobes **37**

28 Superior volsella without microtrichia.. **29**

– Superior volsella covered with microtrichia **32**

29 Dorsal projection weakly developed and undivided; situated posteriorly on tergite IX, close to base of anal point. China, Japan, Thailand...................................... .... ***Nilothauma japonicum* Niitsuma, 1985**

– Dorsal projection well developed, divided or undivided, situated anteriorly on tergite IX, at some distance from base of anal point **30**

30 Dorsal projection three-pronged at apex, without setae. Ghana.......................... .... ***Nilothauma fuscina* Adam & Sæther, 1999**

– Dorsal projection bell-shaped, with numerous setae **31**

31 Superior volsella with single apical seta; anal point narrow. Brazil .... ***Nilothauma matogrossense* Mendes & Andersen, 2009**

– Superior volsella with one dorsolateral and one apical spine-like seta; anal point broad. Ghana .... ***Nilothauma duminola* Adam & Sæther, 1999**

32 Anal point very broad, about half as wide as tergite IX and lanceolate (Fig. 4). Brazil .... ***Nilothauma hamadae* sp. nov.**

– Anal point narrow, spatulate to tapering, but not lanceolate **33**

33 Anal point tapering or only slightly widened medially **34**

– Anal point distinctly spatulate **35**

34 Wing with distinct dark areas at RM, FCu, along apical half of An and in cells r_{4+5} and m_{1+2}. Cuba .... ***Nilothauma granma* Andersen, Bello-González & Hagenlund, 2016**

– Wing without dark areas. Canada, USA .... ***Nilothauma babiyi* (Rempel, 1937)**

35 Dorsal projection large, covering most of tergite IX. Australia .... ***Nilothauma adunatum* Adam & Sæther, 1999**

– Dorsal projection of tergite IX small, with setae at apex only **36**

36 Wing length > 2.4 mm; AR = 0.28; median volsella consisting of two tubercles, each with single, strong apical seta. Canada .... ***Nilothauma verrucum* Adam & Sæther, 1999**

– Wing length < 1.3 mm; AR = 0.13; median volsella consisting of three tubercles, each with strong, apical seta. Venezuela .... ***Nilothauma canaima* Andersen, Bello-González & Hagenlund, 2016**

37 Dorsal projections of tergite IX of the same shape **38**

– Dorsal projections of tergite IX of different shapes **42**

38 Anal point short, digitiform, with microtrichia in basal half; gonostylus distinctly widened in apical one-third. Brazil .... ***Nilothauma zitoi* Mendes & Andersen, 2009**

– Anal point well developed, lanceolate or parallel-sided; gonostylus nearly parallel-sided in apical half **39**

39 Superior volsella short, subtriangular, with two apical tubercles bearing setae; inferior volsella with long, strong simple setae (Fig. 9). Brazil .... ***Nilothauma mateusi* sp. nov.**

– Superior volsella long, pediform to tongue-shaped; inferior volsella with slender, simple apically split setae **40**

40 Anal point parallel-sided; laterosternite IX with thorn. Chile .... ***Nilothauma spiesi* Mendes & Andersen, 2009**

– Anal point lanceolate; laterosternite IX without thorn **41**

41 Inferior volsella and gonostylus with apically split setae; median volsella curved, tapering, with microtrichia and setae. Brazil .... ***Nilothauma jaraguaense* Mendes & Andersen, 2009**

– Inferior volsella and gonostylus with simple setae only; median volsella short, parallel-sided, with two apical setae, without microtrichia. Brazil .... ***Nilothauma amazonense* Mendes & Andersen, 2009**

42 Wing with dark areas or bands; anterior projection on tergite IX long and deeply divided **43**

– Wing without dark markings; anterior projection on tergite IX variably developed **50**

43 Anterior projection on tergite IX with setae not restricted to apex. South Africa . ... ***Nilothauma harrisoni* Adam & Sæther, 1999**

– Anterior projection on tergite IX with apical setae only.................................. **44**

44 Posterior projection on tergite IX deeply divided into antero-dorsal and postero-ventral parts **45**

– Posterior projection on tergite IX not as above **47**

45 Anterior projection on tergite IX with simple, separated, apical setae; anterior part of posterior projection apically pointed; wing with postero-median spot extending on both sides of Cu_1. Afrotropical .... ***Nilothauma pictipenne* Kieffer, 1921**

– Anterior projection on tergite IX with setae forming fan-like structure; anterior part of posterior projection with blunt apex; wing with postero-median spot exclusively proximal of Cu_1 .... **46**

46 Wing with four dark areas; setae on anterior projection on tergite IX branched apically. Ghana........................ ***Nilothauma flabellatum* Adam & Sæther, 1999**

– Wing with three dark areas; apical setae on anterior projection on tergite IX lamellate, not branched. Ghana........ ***Nilothauma kakumense* Adam & Sæther, 1999**

47 Posterior projection on tergite IX either with a disto-dorsal lobe or subapical constriction **48**

– Posterior projection on tergite IX without distal lobe or constriction **49**

48 Posterior projection on tergite IX with long antero-lateral arms and disto-dorsal lobe. Tanzania .... ***Nilothauma anderseni* Adam & Sæther, 1999**

– Posterior projection on tergite IX without antero-lateral arms, with apical constriction and five apical setae. Zimbabwe... .... ***Nilothauma latocaudatum* Adam & Sæther, 1999**

49 Posterior projection on tergite IX without microtrichia, except on long, antero-lateral arms; superior volsella without antero-median extension; median volsella present. China, Japan...................... ***Nilothauma nojirimaculatum* Sasa, 1991**

– Posterior projection on tergite IX without antero-lateral arms, covered with microtrichia; superior volsella with antero-median extension; median volsella apparently absent. Japan .... ***Nilothauma hibaraquartum* Sasa, 1993**

50 Anterior projection on tergite IX with apically plumose setae......................... **51**

– Apical setae on anterior projection on tergite IX not plumose **58**

51 Anal point with microtrichia along median ridge and apical margin. Oriental China............................... ***Nilothauma pandum* Qi, Lin, Wang & Shao, 2014**

– Anal point without microtrichia.. **52**

52 Superior volsella pad-like, with extensive microtrichia. Palaearctic Japan............ .... ***Nilothauma hibaratertium* Sasa, 1993**

– Superior volsella slender, microtrichia absent or limited within small area when present **53**

53 Superior volsella without lateral spur. Thailand .... ***Nilothauma mergae* Adam & Sæther, 1999**

– Superior volsella with lateral spur **54**

54 Superior volsella without setal brush or fringe, with only one to three apical setae **55**

– Superior volsella with apical setal brush or fringe **56**

55 Anal point with microtrichia along median ridge; superior volsella relatively long when compared to median volsella (length ratio, Svo/Mvo > 4.0); inferior volsella with simple setae only. Oriental China .... ***Nilothauma aristatum* Qi, Tang & Wang, 2016**

– Anal point bare; length ratio Svo/Mvo about 2.0; inferior volsella with apically split setae. Oriental China .... ***Nilothauma acre* Adam & Sæther, 1999**

56 Superior volsella four to five times as long as median volsella. Palaearctic Japan .... ***Nilothauma niidaensis* Niitsuma, 2016**

– Superior volsella two to three times as long as median volsella **57**

57 Anterior projection on tergite IX two to four times as long as broad. Canada, USA .... ***Nilothauma bicorne* (Townes, 1945)**

– Anterior projection on tergite IX broader than long. USA .... ***Nilothauma mirabile* (Townes, 1945)**

58 Anal point trifid; anterior projection on tergite IX very long, tapering to parallel-sided apex, with apical setae only; posterior projection on tergite IX distally very slender, with five apical setae. D. R. Congo, Ghana .... ***Nilothauma burmeisteri* Adam & Sæther, 1999**

– Anal point simple; anterior projection on tergite IX wart-like, with setae not only at apex; posterior projection on tergite IX triangular or apically rounded **59**

59 Posterior projection on tergite IX apically rounded; superior volsella with two to four lobes **60**

– Posterior projection on tergite IX triangular; superior volsella without lobes **61**

60 Anterior projection on tergite IX partially divided apically; superior volsella with two lobes. Oriental China .... ***Nilothauma bilobatum* Qi, Tang & Wang, 2016**

– Anterior projection on tergite IX undivided apically; superior volsella with four lobes. Oriental China .... ***Nilothauma quatuorlobum* Yan, Tang & Wang, 2005**

61 Anal point parallel-sided; anterior projection on tergite IX with setae thickened at apices. Ghana .... ***Nilothauma ankasense* Adam & Sæther, 1999**

– Anal point spatulate; anterior projection on tergite IX with setae not thickened at apices **62**

62 Superior volsella tapering, widest near base. Europe .... ***Nilothauma brayi* (Goetghebuer, 1921)**

– Superior volsella widest about one-third from apex. Australia .... ***Nilothauma infissum* Adam & Sæther, 1999**

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Revision of the Afrotropical genus *Fainia* Zumpt, 1958, with notes on the morphology of Rhiniidae subfamilies (Diptera, Oestroidea)

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Abstract

The taxonomy and diversity of *Fainia* Zumpt, 1958, an exclusive Afrotropical genus, had not been reviewed recently. The genus included six nominal species, but the status of several of them was debated. Identification of most *Fainia* species depends on characters of the male terminalia; females are poorly known and, in several cases, are not adequately diagnosed. We conducted a taxonomic revision of the genus and generated identification tools. Based on the study of type material and specimens available in entomological collections in Africa and Europe, we recognise here three of the six species as valid (*F. albitarsis* (Macquart, 1846), *F. elongata* (Bezzi, 1908) and *F. inexpectata* Zumpt, 1973). We also provide an identification key to both sexes, redescriptions of the species, updated distribution records and high resolution photographs of males' and females' habitus and male terminalia. The description of *Fainia kagerana* Lehrer, 2007a **nom. nud.** is an invalid nomenclatural act in terms of ICZN Article 13.1.1. Based on examinations of their holotypes, *F. sambura* Lehrer, 2008 **syn. nov.** is proposed as a junior synonym of *F. albitarsis*; *F. kirinyaga* Lehrer, 2007b **syn. nov.** is proposed as a junior synonym of *F. inexpectata*; and *Fainia giriama* Lehrer, 2007b is moved from the genus *Fainia* to the genus *Rhinia* Robineau-Desvoidy, as *Rhinia giriama* (Lehrer, 2007b) **comb. nov.**. We propose two apomorphies that support the status of the subfamily Rhiniinae.

Keywords

Apomorphies, identification key, nose flies, taxonomy

Introduction

The fly family Rhiniidae, distributed in the Afrotropical, Australasian, Oriental and Palaearctic Regions, includes about 376 described species in 30 genera that have traditionally been placed in two subfamilies: Cosmininae and Rhiniinae (Malloch 1926; Peris 1952, 1992; Pont 1980; Pape et al. 2011). Recent molecular evidence shows that Cosmininae is paraphyletic, separating *Sumatria* Malloch from the rest of the traditional concept of the subfamily Cosmininae, while Rhiniinae is monophyletic (Buenaventura et al. 2020). Rhiniinae includes four genera from the Afrotropical Region: *Fainia* Zumpt, 1958, *Rhinia* Robineau-Desvoidy, *Stomorhina* Rondani and *Vanemdenia* Peris (Zumpt 1962; Kurahashi and Kirk-Spriggs 2006) and is generally recognised by the presence of a long, pectinate antennal arista; reduced dorsal thoracic chaetotaxy; acrostichal and dorsocentral setae that are restricted to the prescutellars pairs; a bare suprasquamal ridge; and a bare proepisternum (Peris 1952, 1992; Zumpt 1958, 1962).

The genus *Fainia* was erected by Zumpt (1958) after the study of two Afrotropical species then assigned to *Idiella* Brauer & Bergenstamm. He distinguished them from the Oriental/Palaearctic *Idiella* species by the unusual shape of the fifth sternite lobes and the fused cerci of the male terminalia. Later, Lehrer (2007a) proposed the subfamily Fainiinae, based on the morphologies of the phallus and the fifth and sixth sternites of *Fainia*, which differed considerably from those of other Afrotropical genera of Rhiniinae. Recent phylogenetic studies place *Fainia* within Rhiniinae as sister-taxon to *Rhinia* (Buenaventura et al. 2020). Prior to that study, *Fainia* comprised six nominal species: *F. albitarsis* (Macquart, 1846), *F. elongata* Bezzi, 1908, *F. inexpectata* Zumpt, 1973, *F. kirinyaga* Lehrer, 2007b, *F. giriama* Lehrer, 2007b and *F. sambura* Lehrer, 2008. However, species of Calliphoridae, Polleniidae and Rhiniidae described by Lehrer need to be revised carefully (e.g. Rognes 2005, 2009, 2011, 2012; Gisondi et al. 2020).

There is very little information on the diversity, biology and distribution of the Rhiniidae. The life cycle and, in particular, the habits and larval morphology are unknown for most of the species (Cuthbertson 1933, 1934; Kurahashi and Kirk-Spriggs 2006; Peris 1952; Zumpt 1958). What is known is limited to a few species that are restricted to specific geographic regions. In general, some species have a strong association with natural environments; adults are flower visitors and are thought to be important pollinators; and some species seem to have a close relationship with termites (Arce et al. 2019; Kurahashi and Kirk-Spriggs 2006; Ferrar 1987).

We present a morphological revision of *Fainia*, including a taxonomic study; an update of nomenclature with morphological considerations of key characters; an identification key; redescriptions; and high quality photographs of males' and females' habitus and male terminalia. We propose two apomorphic characters of the phallus that allow diagnostic differentiation of Rhiniinae.

Material and methods

This study is based in the examination of 59 specimens housed in 10 entomological collections. Available type specimens of the species were examined. The following acronyms were used in the text for the institutions housing the specimens that were examined:

BMSA	Department of Entomology, National Museum, Bloemfontein, South Africa;
CEUA	Entomological Collection, University of Alicante, Alicante, Spain;
DMSA	Durban Natural Science Museum, Durban, South Africa;
MNHN	Muséum National d'histoire Naturelle, Paris, France;
MZSUR	Zoology Museum, La Sapienza University of Rome, Rome, Italy;
NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
SAMC	Iziko South African Museum, Cape Town, South Africa;
SMNHTAU (TAUI)	Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel;
ZMHB	Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany;
ZMUC	Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark.

Morphology and terminology

Morphological characters and terminology follow Cumming and Wood (2017). Male terminalia characters are based on Buenaventura and Pape (2018), Cerretti et al. (2014) and Rognes (1991, 2002, 2009, 2013). Characters of the Rhiniidae male terminalia and fifth sternite are illustrated in Figs 1–3.

Preparation and taxonomic revision of specimens

Pinned and ethanol-preserved specimens were examined using stereomicroscopes (Leica M80 and Leica MZ95) with an ocular micrometer and external LED illumination. Identifications and reidentifications were made following Peris (1952), Zumpt (1958, 1973) and Lehrer (2007a, 2007b, 2008, 2011). Females were identified by morphological comparison with males and the species' descriptions and corroborated using DNA barcodes (Thomas-Cabianca et al., unpublished). Male terminalia were dissected following Rognes (2009) and Cerretti and Pape (2012), stored in small plastic microvials filled with glycerine and pinned or preserved together with their respective specimens. Measurements made in this study are summarised in Fig. 4.

Identification tools

The taxonomic key and descriptions were based on a morphological character matrix built using the DELTA (DEscription Language for TAxonomy) software (Dallwitz 1980a, b, Dallwitz et al. 1999) and building on leads from the DELTA-IntKey module (Dallwitz et al. 2000).

Composite macro-microphotographs

Adult specimens were photographed using a Canon-EOS 6D reflex camera with Canon MP-E 65 mm f/2.8 1–5 lens (ISO 200, f/5.6-9, V:1/160) installed on a copy table with an automatic macro-metric rail and external artificial light or using a Canon-EOS 7D camera with K2-P1CF2 lenses and a P-51 Camlift controller, version 2.8.0.0 (Copyright Roy Larimer/Dun.inc.2014). Photographs included habitus (dorsal and lateral views), head (frontal and lateral views) and abdomen (dorsal and lateral views). Additional photographs of important morphological structures were also taken. Between 15 and 60 high-resolution pictures (in RAW or TIFF format) were taken to cover all of the focal planes needed for focus stacking. Male terminalia were photographed using a stereomicroscope with an integrated Leica M205C camera and coupled DFC450 camera and a Leica Z16AP0A macroscope with coupled Leica DFC490 camera. Photographs included the epandrium, cerci and surstyli (dorsal and lateral view), phallus (lateral, dorsal and ventral view), postgonite and pregonite (lateral view), ejaculatory sclerite (if available) and fifth sternite. Images were processed using Adobe Photoshop Lightroom CS6, stacked with Zerene Stacker, edited with Adobe Photoshop CS6 and measured with IMAGEJ.

Information provided

For each species we provide: valid name, synonyms, diagnosis (included in the identification key), type locality and type repository (including primary types), distribution, biology, redescriptions of male and female, material examined and photographs. Previously unpublished records obtained from the material examined are indicated by an asterisk (*). Some countries are marked with a '?' when the report was a museum database record that showed discrepancies after our examination of the relevant specimen(s).

Citation of specimen label data

Label data of the type material reviewed were recorded verbatim, with information for each line separated by a virgule (/) and labels separated by a double virgule (//). For non-type specimens, the 'material examined' section includes selected information from specimen labels, here presented as: country, province, number of individuals per sex, locality, geographical coordinates, reported elevation, date(s) and collector(s) (leg.), collection method, biological or environmental information, determiner (det.) and date of identification; repository and specimen code (provided by the institution);

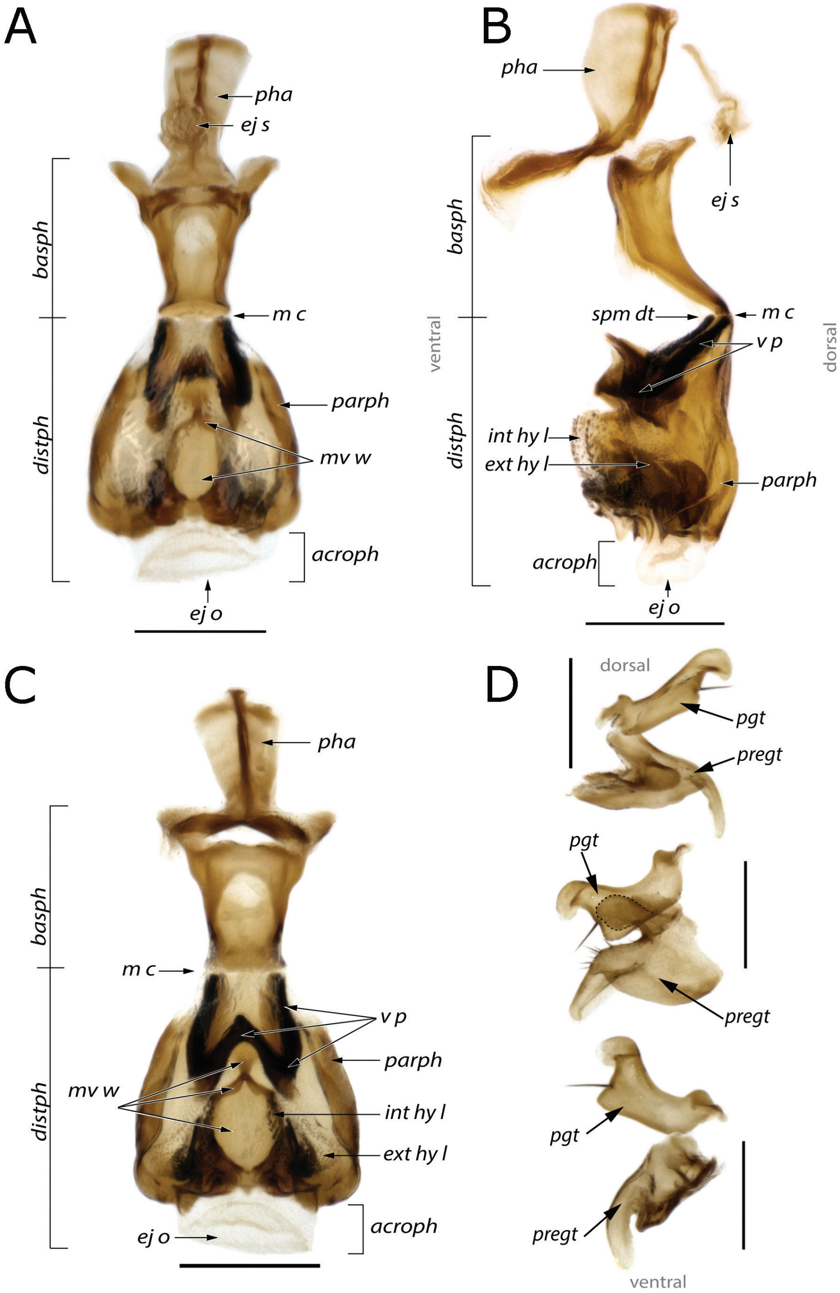

Figure 1. Phallus of *Fainia albitarsis* (Macquart, 1846) **A** dorsal view **B** lateral view **C** ventral view **D** postgonite and pregonite in lateral view. Abbreviations: *acroph* – acrophallus; *basph* – basiphallus; *distph* – distiphallus; *ej e* – ejaculatory sclerite; *ej o* – ejaculatory opening; *ext hy l* – external (distal) hypophallic lobe; *int hy l* – internal (proximal) hypophallic lobe; *m c* – membranous connection; *m w* – mid-ventral wall; *parph* – paraphallus; *pgt* – postgonite; *pha* – phallapodeme; *pregt* – pregonite; *spm dt* – sperm duct; *v p* – ventral plate. Scale bars: 0.2 mm.

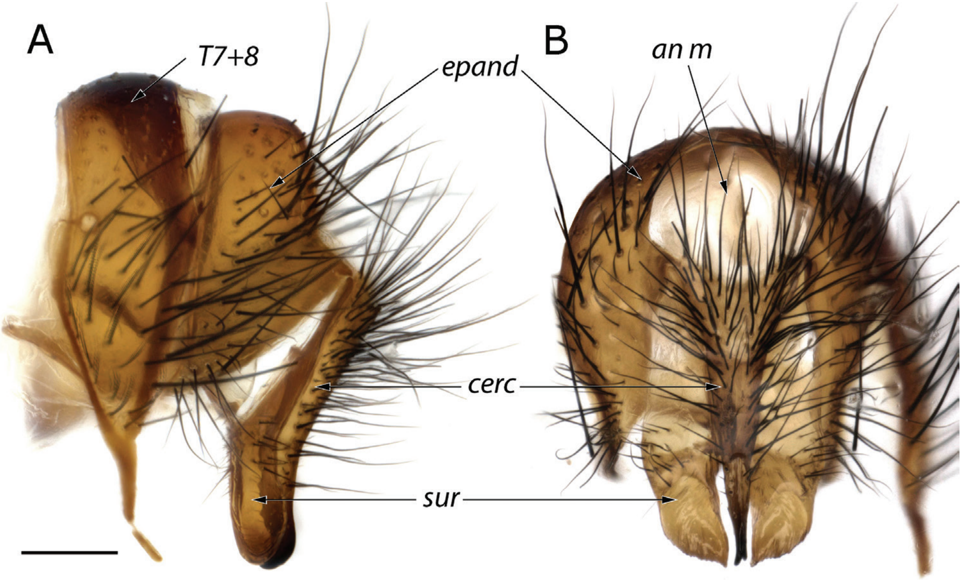

Figure 2. Details of the epandrial complex of *Fainia albitarsis* (Macquart, 1846) **A** lateral view **B** posterior view. Abbreviations: *an m* – anal membrane; *cerc* – cercus; *epand* – epandrium; *sur* – surstylus; *T7+8* – tergite 7 + 8. Scale bar: 0.2 mm.

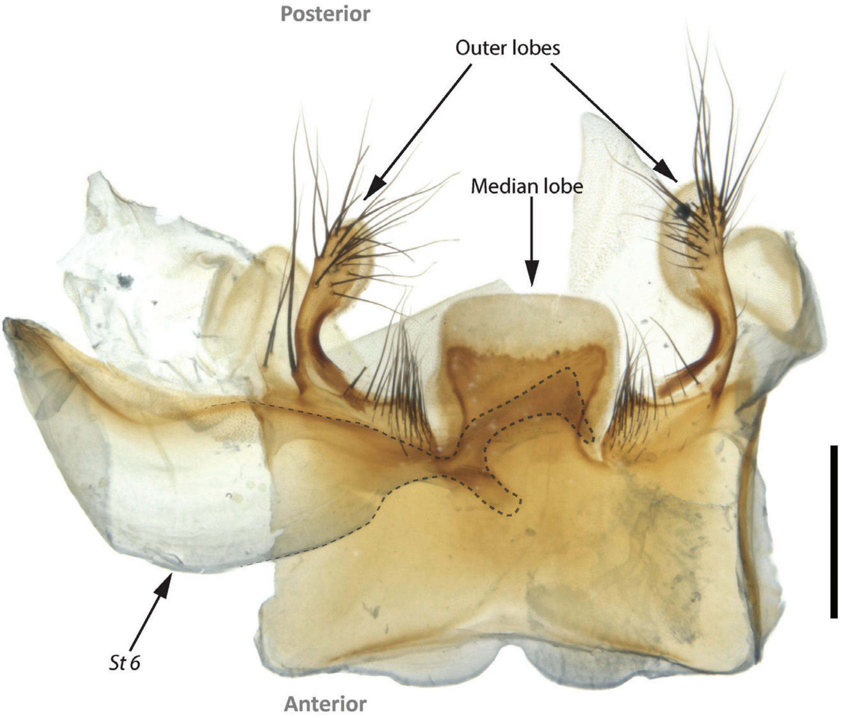

Figure 3. Sternite 5 of *Fainia elongata* (Bezzi, 1908). Abbreviation: *St6* – sternite 6. Scale bar: 0.5 mm.

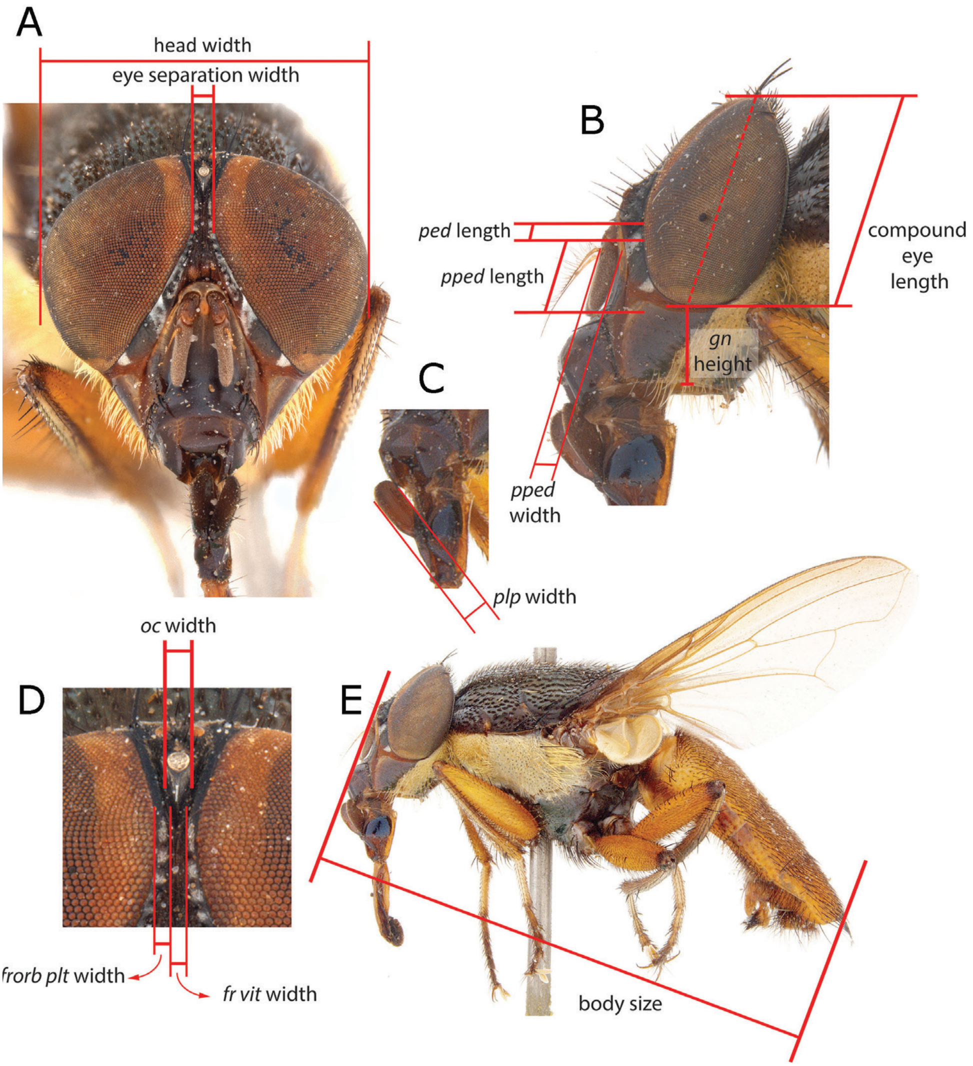

Figure 4. Specification of the characters measured (species = *Fainia albitarsis* (Macquart, 1846)) **A** head in frontal view showing maximum head width and eye separation width **B** head in lateral view showing maximum eye height (spotted red line), maximum gena height, pedicel length and postpedicel length and width **C** palpus in lateral view showing palpus width **D** upper part of head in frontal view showing frontal vitta width, fronto-orbital plate width and anterior ocellus width **E** body size in lateral view. Abbreviations: *fr vit* – frontal vitta; *frorb plt* – fronto-orbital plate; *gn* – gena; *oc* – anterior ocellus; *ped* – pedicel; *plp* – palpus; *pped* – postpedicel.

and male terminalia slide code. Abbreviations used: BECE = Boyekoli Ebale Congo Expedition, HT = holotype, PT = paratype, TS = ♂ terminalia slide, TSP = terminalia slide preparation, KR = Knut Rognes identification database number, ♂ = male, ♂♂ = males, ♀ = female, ♀♀ = females.

Results

Fainia Zumpt, 1958
Figs 1–13

Type species. *Idia albitarsis* Macquart, 1846, by original designation.

Diagnosis. ***Head.*** Arista dorsally pectinate, male eyes separated at narrowest point by less than width of ocellar triangle. ***Thorax.*** Anepisternum with two upper posterior setae and dense yellow microtomentum; katepisternum with or without yellow microtomentum; thoracic chaetotaxy reduced (presutural acrostichal, dorsocentral and intra-alar absent and postsutural acrostichal and dorsocentral setae restricted to prescutellars). ***Legs.*** First tarsomeres always light cream-coloured; fore tibia without submedial posteroventral setae; hind tibia with 2–3 anterodorsal setae as long as tibial diameter, but not forming a distinct row (Fig. 10I). Male mid femur with a distal posteroventral row (ctenidium) of closely spaced spine-like setae (Fig. 5J; this character is also found in some *Stomorhina* species, such as *S. apta* Curran, 1931 and *S. malobana* (Lehrer, 2007c)). ***Wing.*** Cell r_{4+5} always open. ***Male terminalia***. Tergites 5 and 7+8 connected by a long retractile membrane (Fig. 5I), tergite 6 not sclerotised, spiracle 6 present, cerci fused (Figs 2B, 6A, 7A, F, 9A, 11A, 12A) and sternite 5 divided into three posterior lobes (Figs 3, 6F, 7C, I, 9F, 11F, 12F).

Redescription. ♀♂ ***Head*** (Figs 5A–D, 8A–D, 10A–D, 13D–I). Fronto-orbital plate and parafacial ground colour black, covered with silvery microtomentum; parafacial with a glossy black spot; face ground colour black-brown, covered with silvery microtomentum, facial carina protruding (narrow or broad); lower face margin visible in profile, non-rounded, strongly protruding beyond antennal insertion; pedicel and postpedicel ground colour black-brown; arista pectinate, basally yellow and distally dark brown; vibrissa short and thick, 2–4 supravibrissal setulae adjacent to vibrissa; genal dilation anteriorly glossy black and bare, posteriorly covered with dense yellow microtomentum with hairs, generally with tiny piliferous dots around insertion of each hair; occipital area behind postocular setae with a bare and shiny broad black margin. ***Thorax*** (Figs 5G, H, K, L, 8G, K, J, K, 10G, H, J, K, 13A–F). General colouration dark olive green with 3 longitudinal dorsal dark vittae, hair insertions with small piliferous dots; pleura covered by dense yellow microtomentum (in different extension degrees); dorsal chaetotaxy reduced, presutural acrostichal, dorsocentral and intra-alar setae absent and postsutural setae reduced to prescutellars and supra-alar; 2 (outer and anterior) post-postpronotal setae present, postalar wall and suprasquamal ridge bare. ***Wing*** (Fig. 4E). Cell r_{4+5} always open. ***Legs*** (Figs 5J–L, 8J, K, 10I–K). Femora reddish-yellow; male mid-femur bearing a distal posteroventral row (ctenidium) of closely spaced setae (Fig. 5J) that are spine-like in male but not in female; tibiae yellow to brown; first tarsomeres creamy white; first and second hind tarsomeres creamy, almost white. ***Abdomen*** (Figs 5E, F, K, L, 8E, F, J, K, 10E, F, J, K). Longer than broad, extending to wing tip or even further; colour generally yellow-orange and sometimes partly brown. ***Male terminalia*** (Figs 1–3, 6, 7, 9, 11, 12). Sternite 5 divided into three posterior lobes, 2 outer and 1 median. Outer lobes elongated and posteriorly slender or broad, tending to an inward curve (Figs 3, 6F, 7C, I, 9F, 11F, 12F), with or without abundant setae of different lengths and thickness; medial lobe forming a broad protuberance of varied shape (Figs 3, 6F, 7C, I, 9F, 11F, 12H). Phallus with basi- and distiphallus not fused and connected through a membrane (connection membrane) (Fig. 1A–C); epiphallus absent; basiphallus with two anterolateral processes; ventral plate articulate; paraphallus distally globular.

Key to *Fainia* species

1 Thorax with katepisternum partially or completely covered with dense yellow microtomentum, meron with lighter yellow microtomentum (Fig. 10J, K). ♂ Hind tibia with 2 anterodorsal setae and 2 posterodorsal setae.................... **2**

– Thorax with katepisternum and meron glossy or covered with a light yellow-silvery microtomentum (Fig. 5K, L). ♂ Hind tibia with 3 anterodorsal setae and 3 posterodorsal setae. ♂ Eyes separated at narrowest point by 1.50 to 2.00 times width of anterior ocellus (Fig. 5A); abdominal sternite 5 with outer lobes covered with thick hairs and median lobe with a rounded, protruding posterior margin (Fig. 6F). ♀ Abdomen with posterior margin of tergite 5 without an emargination and with a row of thin, sparse, black marginal setae (Fig. 5F) .... ***F. albitarsis* (Macquart, 1846)**

2 Katepisternum completely covered with dense yellow microtomentum, as on anepisternum (Fig. 8J, K). ♂ Eyes separated at narrowest point by 0.75 to 1.30 times width of anterior ocellus (Fig. 8A); abdominal sternite 5 with long outer lobes covered by long hairs, median lobe square with straight posterior margin (Fig. 9F). ♀ Abdomen with posterior margin of tergite 5 with a triangular emargination (inward) and with a row of thick, long, black marginal setae (Fig. 8F) .... ***F. elongata* (Bezzi, 1908)**

– Katepisternum not completely covered with dense yellow microtomentum (as on anepisternum), which is restricted to upper half (Fig. 10J, K). ♂ Eyes separated at narrowest point by 1.50 to 2.00 times width of anterior ocellus (Fig. 10A); abdominal sternite 5 with short and curved outer lobes covered by a few thin hairs; median lobe almost triangular (broken or not in the middle of posterior margin) (Figs 11F, 12F, H). ♀: Abdomen with posterior margin of tergite 5 without an emargination and with a row of thick, short, black marginal setae (Fig. 10F).................................. ***F. inexpectata* Zumpt, 1973**

***Fainia albitarsis* (Macquart, 1846)**

Figs 1, 2, 4, 5, 6, 7, 13B, C, E, F, H, I

≡ *Idia albitarsis* Macquart, 1846: 321 (*teste* Zumpt 1958)
= *Idia eupoda* Loew, 1852: 660 [redescribed 1862: 24] (*teste* Peris 1952; Zumpt 1958)
= *Idia extensa* Walker, 1858: 211 (*teste* Peris 1952; Zumpt 1958)

= *Fainia kagerana* Lehrer, 2007a: 2 nom. nud. (no differential diagnosis)
= *Fainia sambura* Lehrer, 2008: 16 syn. nov.

Type localities and repositories of primary types. *Idia albitarsis*: South Africa, Caferie [= KwaZulu-Natal], (?co)Type(s) female(s) in MNHN (destroyed, not in remnants of the Macquart Collection, Thomas-Cabianca, pers. obs., lateral head view illustrated in Macquart 1846: plate 17, figure 2). *Idia eupoda*: Mozambique, Inhambane, (?co)Type(s) [female(s)] in ZMHB (number of type specimens not specified, not located, considered missing, Thomas-Cabianca, pers. obs.; sex and locality specified in Loew (1862: 24)). *Idia extensa*: South Africa, Port Natal [= Durban], (?co) Type(s) male(s) in NHMUK (Natural History Museum UK) (number of type specimens not specified, not examined). *Fainia sambura*: Kenya, Taita Hills, male HT in SMNHTAU (TAUI) (examined).

Distribution. Central African Republic, Democratic Republic of the Congo, ?Ghana, Kenya, Malawi, Mozambique, Namibia, Sierra Leone, South Africa, Sudan, Tanzania, Uganda, Zimbabwe (Peris 1952, 1956; Zumpt 1958; Pont 1980; Kurahashi and Kirk-Spriggs 2006; Lehrer 2011).

Biology. Ecology, immature stages and life history unknown.

Redescription (male and female). Length 7.83 mm [6.55–9.00 mm] (n = 9). ***Head*** (Fig. 5A–D). ***Thorax*** (Fig. 5G, H, K, L). Chaetotaxy: acrostichal setae = 0 + 1, dorsocentral setae = 0 + 1, intra-alar setae = 0 + 1, postpronotal lobe setae = 1 long and sometimes 1 extra short, outer post-postpronotal lobe setae present, presutural seta present, supra-alar setae = 2, marginal scutellar setae = 3, discal scutellar setae = 0, proepisternal setae = 2, proepimeral seta = 0. Katepisternum covered with light silvery microtomentum; proepimeron, proepisternum, anepimeron, anepisternum and inferior half of postpronotal lobe covered with dense yellow microtomentum (Fig. 5K, L), anepisternal setae = 2 anterior to an extra posterior dense row of yellow hairs (Fig. 5K, L). ***Wing*** (Fig. 5K, L). Tegula and basicosta black-brown, outer margin along costal vein lightly infuscated. Lower calypter yellow and slightly longer than broad. ***Legs*** (Fig. 5K, L). Femora yellow-orange, tibiae yellow to brown. ***Abdomen*** (Fig. 5E, F, K, L). Yellow-orange, longer than broad. **Male** (n = 8). ***Head*** (Fig. 5A, C). Eye bare, inner facets moderately enlarged, but not demarcated from outer ones. Eyes separated by 0.06 times width of head [0.05–0.06] (at narrowest point, one-half to two times width of anterior ocellus); eye length 2.99 times height of gena [2.70–3.16]. Postpedicel length 2.39 times length of pedicel [2.10–2.27]; ocellar setae well-developed, inner vertical seta present, outer vertical seta absent; 6–8 frontal setae; palpus width around 2 times width of postpedicel in broadest area. ***Legs.*** Fore tibia 1–2 anterodorsal setae; mid-tibia 1 anterodorsal seta, 1 posterodorsal seta; hind tibia 2 anterodorsal setae, 2 posterodorsal setae, 2 anteroventral setae. ***Abdomen.*** *Terminalia* (Fig. 6). Median lobe width 0.33 times the width of sternite 5, posterior margin round with a lighter and less sclerotised margin; section that connects with outer lobes covered with scattered black hairs. Outer lobes shorter and broader than in *F. elongata* (Fig. 9F), terminal area

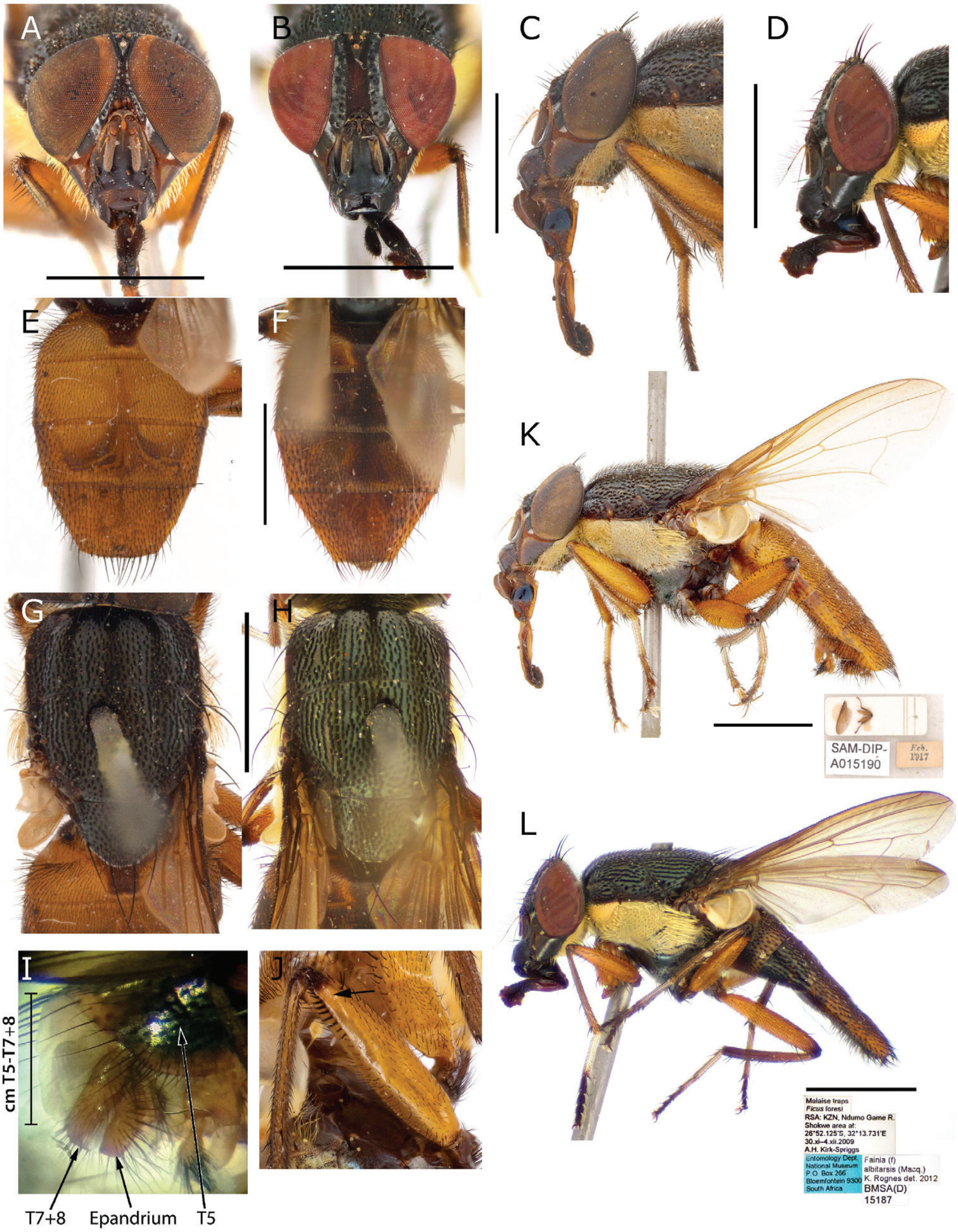

Figure 5. *Fainia albitarsis* (Macquart, 1846), general body views of male (SAM DIP A015190) and female (BMSA (D) 15187) **A, C, E, G, I–K** male **A** head in frontal view **C** head in lateral view **E** abdomen in dorsal view **G** thorax in dorsal view **I** retractile membrane connecting *T5* and *T7+8* **J** mid-femur, showing posteroventral row of closely spaced spine-like setae distally **K** lateral habitus and labels **B, D, F, H, L** female **B** head in frontal view **D** head in lateral view **F** abdomen in dorsal view **H** thorax in dorsal view **L** lateral habitus and labels. Abbreviations: *cm T5-T7+8* – connective membrane between tergite 5 and 7+8, *T5* – tergite 5, *T7+8* – tergite 7+8. Scale bars: 2 mm.

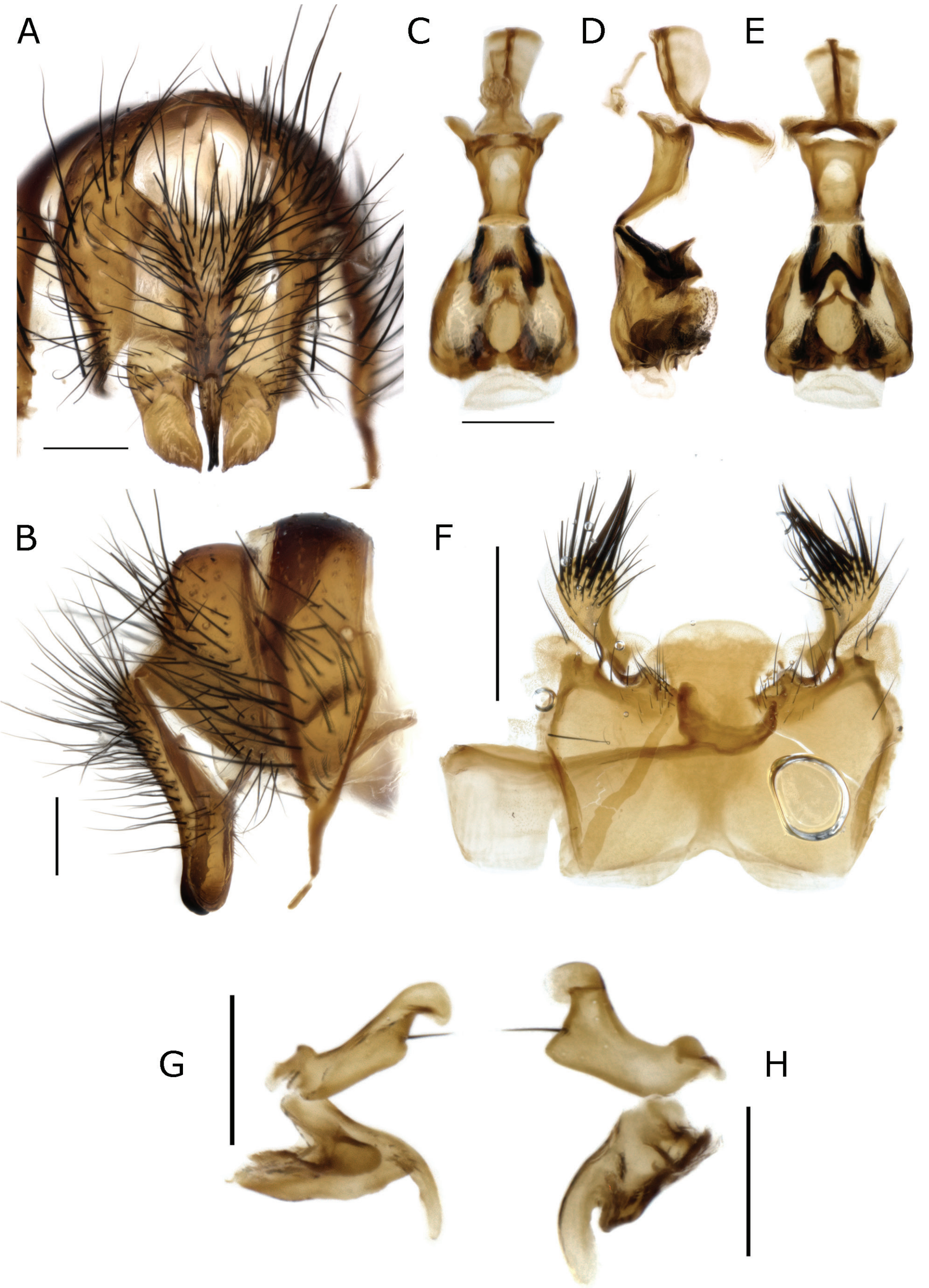

Figure 6. *Fainia albitarsis* (Macquart, 1846), male terminalia (BMSA (D) 30066) **A, B** epandrial complex and tergite 7+8 in dorsal (**A**) and lateral (**B**) view **C–E** phallus in dorsal (**C**), lateral (**D**) and ventral (**E**) view **F** sternite 5 in ventral view and **G, H** postgonite (upper) and pregonite (lower) in lateral-external (**G**) and lateral-internal view (**H**). Scale bars: 0.2 mm.

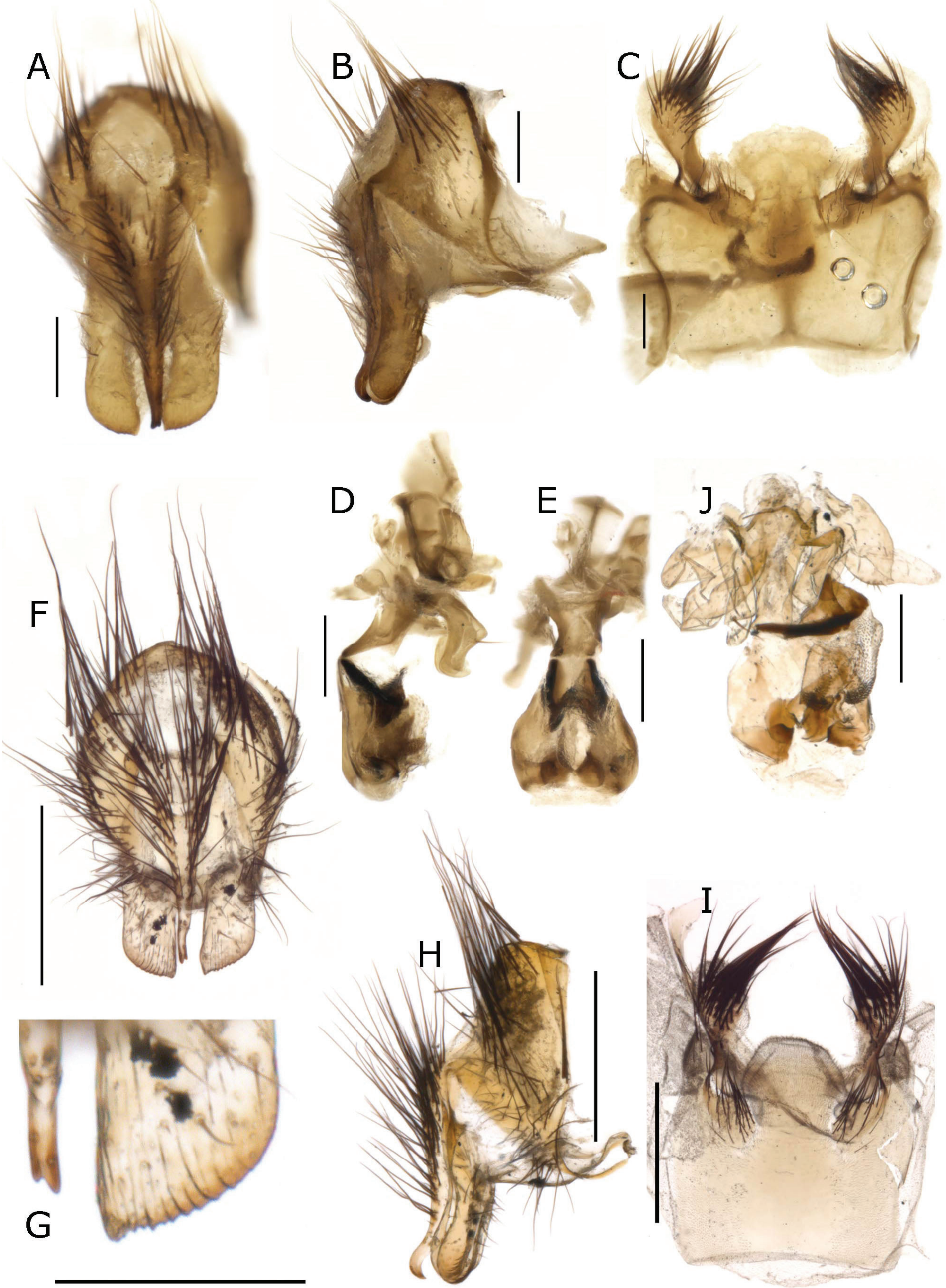

Figure 7. *Fainia kagerana* Lehrer, 2007a nom. nud. (SMNHTAU (TAUI) 318988) and *Fainia sambura* Lehrer, 2008 holotype (SMNHTAU (TAUI) 318990), male terminalia **A–E** *F. kagerana* **A, B** epandrial complex in dorsal (**A**) and lateral (**B**) view **C** sternite 5 in ventral view and **D, E** phallus in lateral (**D**) and ventral (**E**) view **F–J** *F. sambura* **F–H** epandrial complex in dorsal view (**F**), details of surstylus, showing serrations along distal margin (**G**) and lateral view (**H**) and details in **I** sternite 5 in ventral view **J** phallus view. Scale bars: 0.2 mm.

globular and covered with long and thick black setae, surrounded by a lighter halo with dense yellow vestiture. Surstylus wide and rectangular (plate form), slightly curved outward in medial distal edge (Fig. 6A), posterior edge serrated and grooved (Figs 6A, 7G); ventrally and dorsally covered with black hairs in medial area. Cercus slender and fused, with long black setae, apically bifurcated (Figs 6A, 7G) forming an inward hook in lateral view (Fig. 7H). Phallus as Figs 6C–E, 7D, E, ventral plate in ventral view M-shaped (which is obvious (Figs 1C, 6E) or not, depending of ventral plate position); postgonite and pregonite as in Fig. 6G, H. **Female** (n = 1). ***Head*** (Fig. 5B, D). Eyes separated 0.23 times of the head width at the narrowest point; eye length 4.14 times gena height; postpedicel 2.21 times pedicel length; proximal edge of fronto-orbital plate weakly concave towards frontal vitta; fronto-orbital plate 0.58 times frontal vitta width at ocellar triangle tip; ocellar setae well-developed and proclinate, 7–8 frontal setae, 2 proclinate orbital setae, 1 reclinate orbital seta; palpus width more than 3.00 times postpedicel width in broadest area. ***Legs.*** Fore tibia 2 anterodorsal setae; mid-tibia 1 anterodorsal seta, 1 posterodorsal seta, 1 anteroventral seta, 2 posteroventral setae; hind tibia 2 anterodorsal setae, 1–2 posterodorsal setae, 2 anteroventral setae. ***Abdomen*** (Fig. 5F, L). Posterior margin of tergite 5 without emargination, marginal setae thin and black.

Discussion. *Fainia albitarsis* is widely distributed in the Afrotropical Region. It was adequately diagnosed by Peris (1952) and redescribed by Zumpt (1958), but the illustrations of sternite 5 are incongruent between the two authors. Photographs of sternite 5 (Fig. 6F) are provided here for a proper determination of the species. The HT or STs were found to be destroyed by pests at MNHN. Additionally, the HT or STs of *F. eupoda* were not found in ZMHB and we consider it missing. The specimen assigned as HT of *Idia eupoda* in ZMHB is labelled as '*Pr. b. sp* Krebs // 4532 // Type (red-label) // *eupoda* Loew*'; '*Pr. b. sp*' refers to *Promontorium bonae spei*, Latin for "Cape of Good Hope" in South Africa and it was collected by Ludwig Krebs (1792-1844), Cape naturalist to the King of Prussia. This differs from the published type locality and collector: Inhambane, Mozambique leg. Peter, suggesting that the specimen is, in fact, not a type. Specimens from Democratic Republic of the Congo, Kenya and South Africa (see material examined section) identified by Knut Rognes, together with the description of Zumpt (1958), were used for the proper determination of this species. As the descriptions were adequate for identification, neotypes are not required for *Fainia albitarsis* or *Idia eupoda*. The synonymy of *Idia extensa* was first published by Peris (1952), and seems reliable.

The description of *Fainia kagerana* nom. nud. is an invalid nomenclatural act in terms of ICZN Article 13.1.1 because it lacks a comparative diagnosis. In addition, the descriptions and drawings of *F. kagerana* nom. nud. (Lehrer 2011: 59–61) (Fig. 13C, E, I) and *F. sambura* syn. nov. (Lehrer 2011: 63–65) (Fig. 13B, F, H) match the morphology of *F. albitarsis*. On examining the *F. sambura* syn. nov. HT, including the male terminalia (dissected by Lehrer) (Fig. 7), we found that the surstyli, cerci and ventral plate exhibit the same diagnostic characters as described above (Fig. 6A, B). Careful examination of the ventral plate of the phallus revealed that the structure is articulated, with the joint located within the basi- and distiphallus membranous connection. This articulation can produce different orientations of the ventral plate in lateral and ventral views of the phallus, obscuring their typical 'M' shape visible in ventral view in various specimens. The phallus drawings of *F. kagerana* nom. nud. (Lehrer 2011: fig. 36D) and *F. sambura* syn. nov. (Lehrer 2011: fig. 39D) show different orientations of the ventral plate in lateral view, suggesting that they could be different species. The 'M' shape of the ventral plate can be clearly observed in the specimen of *F. kagerana* nom. nud. (Figs 6E, 7E) and partially observed in the HT of *F. sambura* syn. nov. as it was partially damaged (it was crushed between the lid and wall of the microvial) (Fig. 7J). Based on this evidence, we conclude that *F. sambura* is synonym of *F. albitarsis* and *F. kagerana* nom. nud. corresponds to *F. albitarsis*.

Type material examined. *Fainia sambura* HT. 1 ♂ KENYA: Taita Hills / 1000–1200 m / Wyundani Rd. 3°24'S, 38°23'E / 18.ix.2005 / L. FRIEDMAN // holotypus // n. sp. / det. Dr A.Z. Lehrer // SMNHTAU (TAUI) 318990.

Other material examined. 19 specimens (10 ♀♀ 9 ♂♂).

Democratic Republic of the Congo – Katanga • 1 ♂; Ubani Valley Umbombo Dist.; Mar. 1915; Yoppin leg., det. Thomas-Cabianca, A., 2018; DMSA DIP 6260. – **Oriental** • 1 ♀; Bomane village area; 01°16.283'N, 23°43.994'E; 24 May 2010; Kirk-Spriggs, A.H. leg.; lowland evergreen second dry forest; Malaise trap; det. Rognes, K., 2012; BMSA-BECE 01314.

Kenya – Coast • 1 ♀; N. edge of Arabuko Sokoke Forest; UTM 37 M 607257 9644873, 83 m elev.; 28 May 2006; Avesani, D., Carpaneto, G., Nardi, G. & Cerretti, P. leg.; hand net; with larva, det. Rognes, K.; MZSUR – **Nairobi** • 1 ♀; Kakura Forest; 01°14'28.64"S, 36°49'54.97"E; 1672 m elev.; 21–23 Nov. 2017; PINDIP-Course leg.; Kenyan dry forest; 6 m elev. Malaise trap; det. Thomas-Cabianca, A., 2017; CEUA, DNA-COI USA04 • 1 ♂, same collection data as previous; 23 Nov. 2017; general sweeping; CEUA, DNA-COI USA03.

South Africa – KwaZulu-Natal • 1 ♂; Amatigulu Nature Reserve, north of Tugela River mouth; 29°12'S, 31°36'E; 25–26 Aug. 2006; Davies, G.B.P. leg.; caught hovering in group; det. Thomas-Cabianca, A., 2018; NMSA DIP 84325 • 1 ♀; Durban; 1914; Haygarth, W.J. leg.; det. Villeneuve (as *Idiella eupoda*); SAMC DIP A015193 • 1 ♂; Manguzi Forest Reserve; 26°59'32"S, 32°43'25"E; 61 m elev.; 13–17 Dec. 2010; Kirk-Spriggs, A.H. leg.; indigenous sand forest; Malaise trap; det. Rognes, K., 2012; BMSA (D) 30066 • 1 ♀; Ndumo Game Reserve, Red Cliffs/Shokwe area at Ingwavuma; 26°52.125'S, 32°13.731'E; 30 Nov.–04 Dec. 2009; Kirk-Spriggs, A.H. leg., *Ficus* forest; Malaise trap; det. Rognes, K., 2012; BMSA (D) 15187 – **Mpumalanga** • 1 ♀ 1 ♂; Blyde River, Burkes Luck; 24°40'30"S, 30°48'40"E; 1200 m elev.; 24 Dec. 1990; Roth, V. & Roth, B. leg.; det. Thomas-Cabianca, A., 2018; NMSA DIP ♀: 84327 ♂: 84332 – **Western Cape** • 2 ♂♂; George (Caplant); 01 Feb. 1918; Brauns, Dr H. leg.; det. Thomas-Cabianca, A., 2018 (previously determined as *Rhinia apicalis* in the collection); NMSA DIP 020015 • 1 ♀; *Pr. B. sp.*; Krebs leg.; det. Loew (previously determined as *Fainia eupoda* in the collection); ZMHB HT 4532.

Tanzania – Morogoro • 1 ♀; Udzungwa Mountains National Park, Mito Mitato Plot 13; 674 m elev.; 26 Oct. 2014; Malumbre-Olearte, J. leg.; det. Thomas-Cabianca,

A., 2019; ZMUC, DNA-COI K3 • 1 ♀ 2 ♂♂; Udzungwa Mountains National Park, Mizimu Camp.; 769 m elev.; 01 Sep. 2013; Pape, T. & Scharff, N. leg.; det. Thomas-Cabianca, A., 2019; ZMUC, ♀: DNA-COI K7, ♂♂ DNA-COI K6 K20 **– Tanga •** 1 ♂; Usambara, Mts., Rt. B124, 1300 m elev., near Lushoto; 10–15 Sep. 1992; Freidberg, A. leg; det. Thomas-Cabianca, A. 2019; (previously determined as *Fainia kagerana* HT by Dr A.Z. Lehrer, 2007 in the collection); SMNHTAU (TAUI) / 318988.

***Fainia elongata* (Bezzi, 1908)**

Figs 3, 8, 9

≡ *Stomatorrhina elongata* Bezzi, 1908: 383 (*teste* Zumpt 1958)
= *Idiella major* Malloch, 1926: 510 (*teste* Peris 1952; Zumpt 1958)

Type localities and repositories of primary types. *Stomatorrhina elongata*: Bas-Congo (= Democratic Republic of the Congo), male HT in IRSNB (Royal Belgian Institute of Natural Sciences, Brussels, Belgium) (description based on a single male specimen, not examined). *Idiella major*: Sierra Leone, Masimera to Yonnibanna, (?co)Type(s) female(s) in NHMUK (Natural History Museum UK) (number of type specimens not specified, locality specified in Peris (1952: 48), not examined).

Distribution. Cameroon, Central African Republic*, Democratic Republic of the Congo, Equatorial Guinea, Ivory Coast, Kenya, ?Madagascar, Malawi, Mozambique, Namibia, ?Nigeria, Rwanda, Sierra Leone, South Africa, Sudan, Tanzania, Togo, Uganda, Zimbabwe (Malloch 1926; Peris 1952, 1956; Zumpt 1958, 1962; Pont 1980; Kurahashi and Kirk-Spriggs 2006).

Biology. Ecology, immature stages and life history unknown.

Redescription. Length 10.76 mm [10.60–10.87] (n = 3) ***Head*** (Fig. 8A–D). ***Thorax*** (Fig. 8G–K). Acrostichal setae = 0 + 1, dorsocentral setae = 0 + 1, intra-alar setae = 0 + 1, post postpronotal lobe setae = 1 long and 1 short, outer post postpronotal lobe seta present, supra-alar setae = 2, marginal scutellar setae = 3, discal scutellar setae = 0, proepisternal setae = 2, proepimeral seta = 0. Proepimeron, proepisternum, anepimeron, anepisternum, katepisternum and inferior half of postpronotal lobe covered with dense yellow microtomentum (Fig. 8J, K); meron also covered, but with microtomentum lighter, anepisternal setae = 2 anterior to an extra dense row of yellow hairs (Fig. 8J, K). ***Wing***. Tegula and basicosta black-brown, outer margin along costal vein light infuscate, lower calypter yellow and slightly longer than broad. ***Legs*** (Fig. 8J, K). Femora yellow, tibiae yellow to brown. ***Abdomen*** (Fig. 8E. F). Yellow-orange, longer than broad. **Male** (n = 2). ***Head*** (Fig. 8A, C). Eye bare, inner facets moderately enlarged but not demarcated from outer ones. Eyes separated by 0.04 times width of head [0.04–0.04] (at narrowest point between 1.10 to 1.30 times anterior ocellus width); eye length 3.51 times height of gena [3.49–3.54]. Postpedicel length 2.52 times length of pedicel [2.44–2.61], ocellar setae well-developed, inner vertical seta present, outer vertical seta absent, 8-10 frontal setae, palpus width in broadest area around 2.50 times width of

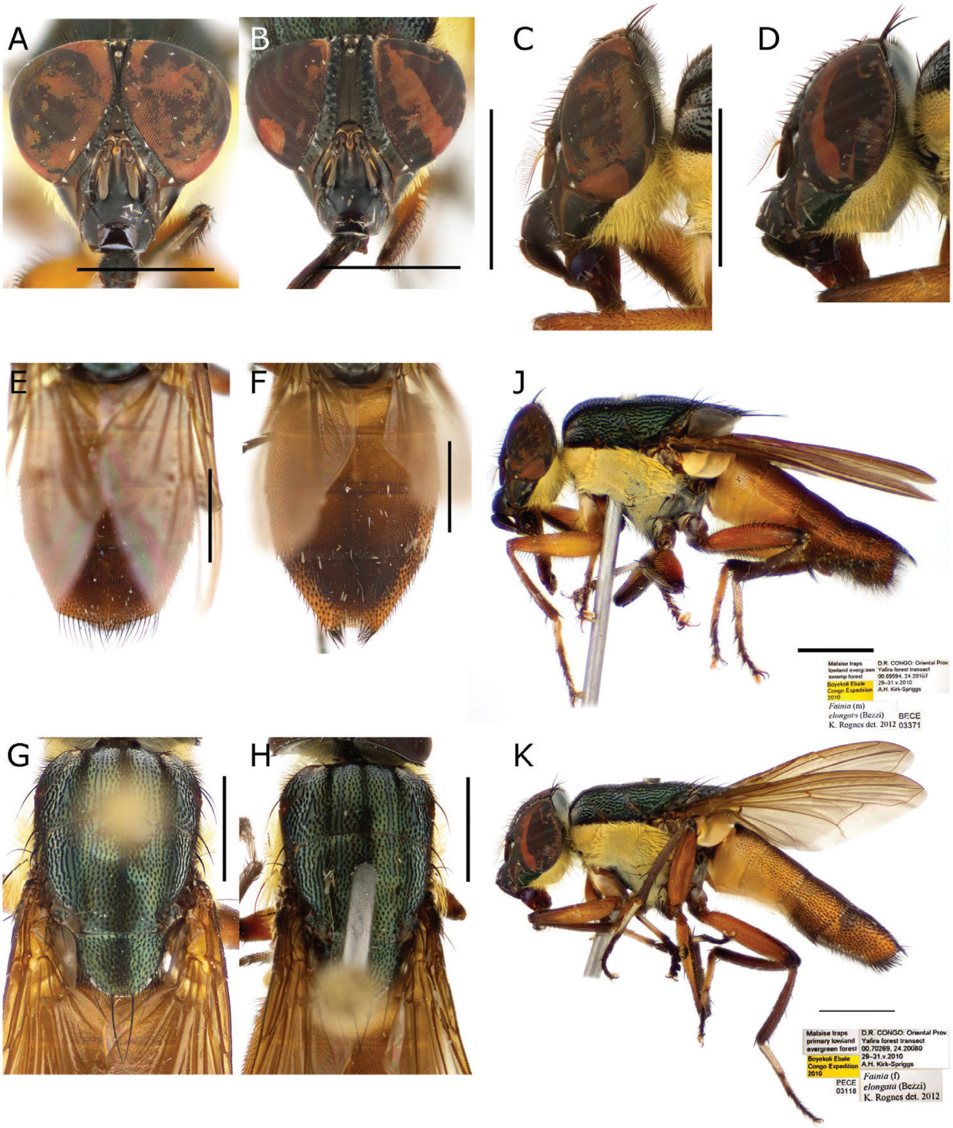

Figure 8. *Fainia elongata* (Bezzi, 1908). General body views of male (BMSA-BECE 03371) and female (BMSA-BECE 03118) **A, C, E, G, J** male **A** head in frontal view **C** head in lateral view **E** abdomen in dorsal view **G** thorax in dorsal view **J** lateral habitus and labels **B, D, F, H, K** female **B** head in frontal view **D** head in lateral view **F** abdomen in dorsal view **H** thorax in dorsal view **K** lateral habitus and labels. Scale bars: 2 mm.

postpedicel. ***Thorax*** (Fig. 8G, J). ***Legs*** (Fig. 8J). Fore tibia with 2–3 anterodorsal setae; mid-tibia with 1 anterodorsal seta, 1 posterodorsal seta; hind tibia with 3 anterodorsal setae (row-like), 3 posterodorsal seta (row-like), 2 anteroventral setae. ***Abdomen*** (Fig. 8E, J). ***Terminalia*** (Fig. 9). Medial lobe 0.5 times width of sternite 5, posterior

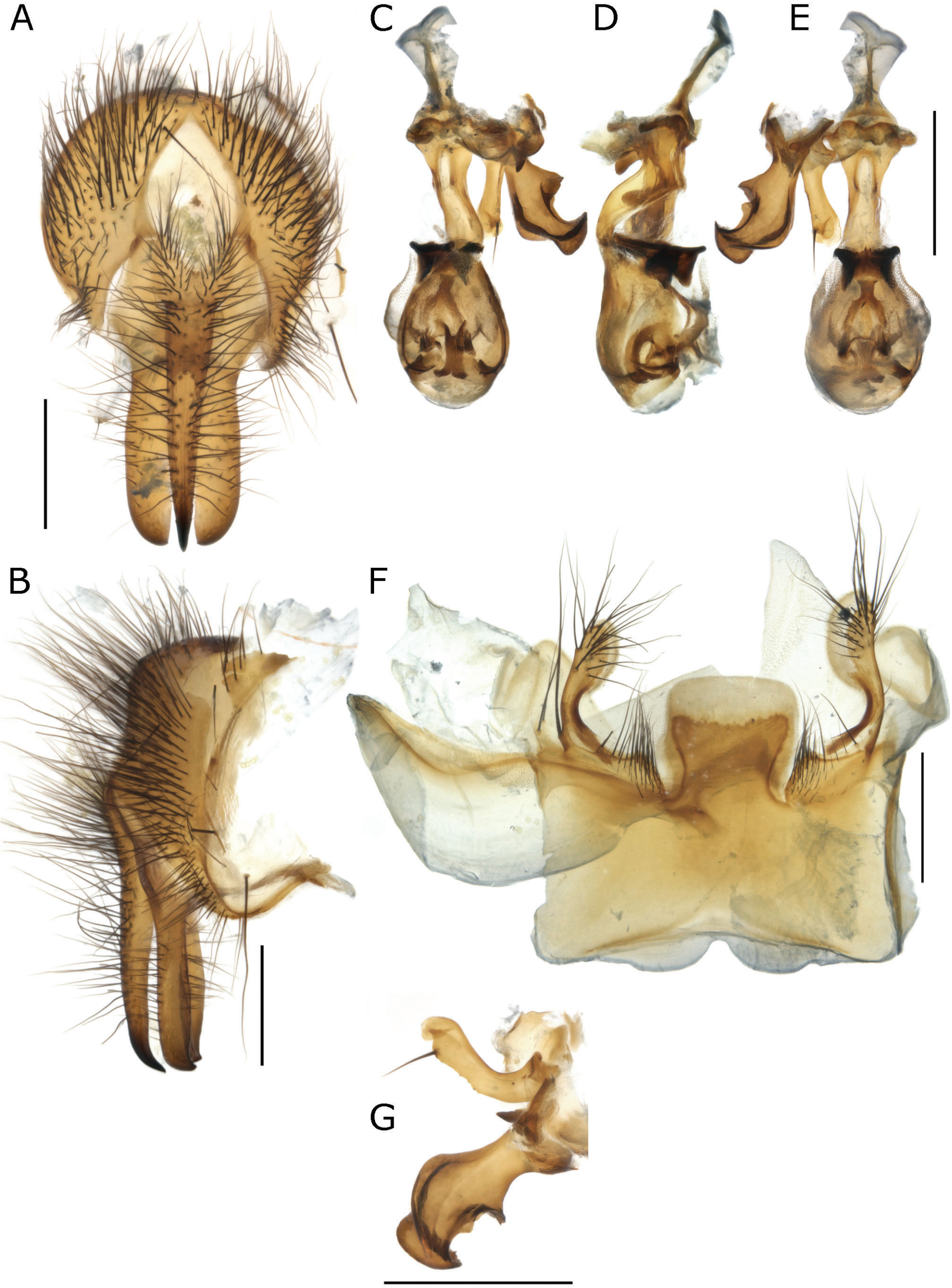

Figure 9. *Fainia elongata* (Bezzi, 1908). Male terminalia (BMSA-BECE 03371) **A, B** epandrial complex in dorsal (**A**) and lateral (**B**) view **C–E** phallus in dorsal (**C**), lateral (**D**) and ventral (**E**) view **F** sternite 5 in ventral view and **G** postgonite (upper) and pregonite in lateral-external view (**G**). Scale bars: 0.2 mm.

margin straight or almost straight and less sclerotised, area that connects with outer lobes densely covered by black hairs (Fig. 9F). Outer lobes longer and narrow, curved in proximal direction (like an open 'C'), terminal area round, covered by long and thick black setae, surrounded by a lighter halo with yellow vestiture (Fig. 9F). Sustylus rectangular (Fig. 9A, B), thinner and more slender than in *F. albitarsis* (Fig. 6A, B), posterior area darker (Fig. 9A, B), ventrally and dorsally with black setae (Fig. 9A, B), in lateral view (Fig. 9B) slightly curved inwards at ventral posterior region and proximally pointed (Fig. 9B). Cercus slender and fused, covered with long black setae, forming an inward hook apically (Fig. 9B). Phallus as in Fig. 9C–E, ventral plate in ventral view as in Fig. 9E; postgonite and pregonite as in Fig. 9C–E, G. **Female** (n = 1). ***Head*** (Fig. 8B, D). Eyes separation 0.20 times width of head**,** eye length 3.12 times height of gena. Postpedicel 2.08 times length of pedicel; frontal vitta subparallel-sided; fronto-orbital plate 0.60 times as wide as frontal vitta at tip of ocellar triangle; ocellar setae well-developed and proclinate, 11 frontal setae, 5 or more proclinate orbital setae, 1 reclinate orbital seta; palpus width more than 2.00 times postpedicel width in broadest area. ***Thorax*** (Fig. 8H, K). ***Legs*** (Fig. 8K). Fore tibia 2 anterodorsal setae; mid-tibia 1 anterodorsal seta, 1 posterodorsal seta, 1 anteroventral seta, 2 posteroventral setae; hind tibia 2 anterodorsal setae, 2 posterodorsal setae, 2 anteroventral setae. ***Abdomen*** (Fig. 8F, K). Tergite 5 with a triangular middle incision (Fig. 8F).

Discussion. We were not able to examine the type material of *Fainia elongata* or *Idiella major*, but *F. elongata* is a well-defined species, properly described by Bezzi (1908) and diagnosed by Peris (1952) and Zumpt (1958). The synonymy was first published by Peris (1952) and seems reliable.

Material examined. 21 specimens (7 ♀♀ 14 ♂♂).

Cameroon • 1 ♂; Páma-Quelle, Lobaje, Marsch am-Ubangi (Neu-Kamerun); 1913; Ramsay, S.G. leg.; det. Zumpt, F., 1955; ZMHB Dipt S06219 TS no. 19 • 1 ♂; Páma-Quelle (Neu-Kamerun); 1913; Ramsay, S.G. leg.; det. Zumpt, F., 1955; ZMHB Dipt S06219 TS no. 3; • 1 ♀ 2 ♂♂; Páma-Quelle, Lobaje // Marsch am-Ubangi (Neu-Kamerun); 15 Feb. 1913; Ramsay, S.G. leg.; det. Thomas-Cabianca, A., 2019; ZMHB Dipt ♀: S06217 ♂♂: S06219 • 1 ♂; Páma-Quelle // Mboko (Neu-Kamerun); 23 Feb. 1913; Ramsay, S.G. leg.; ZMHB Dipt S06219.

Central African Republic – Sangha-Mbaéré • 5 ♂♂; Parc National de Dzanga-Ndoki, Mabéa Bai, 21.4 Km 53'NE Bayanga; 3°02.01'N, 16°24.57'E; 510 m elev., 03–04 May 2001; van Noort, S. leg.; marsh clearing; lowland rainforest; Malaise trap; det. Thomas-Cabianca, A., 2018; SAMC DIP A015267 • 1 ♂; Parc National de Dzanga-Ndoki, 38.6 km 173'S Lidjombo; 2°21.60'N, 16°09.20'E; 350 m elev.; 21–22 May 2001; van Noort, S. leg.; lowland rainforest; Malaise trap; det. Thomas-Cabianca, A., 2018; SAMC • 1 ♀ 2 ♂♂; same collection data as previous; 23–24 May 2001; SAMC DIP ♀: A015266; ♂: A015269.

Democratic Republic of the Congo – Oriental • 1 ♀; Yafira Forest transect; 0.70269'N, 24.20080'E; 29–31 May 2010; Kirk-Spriggs, A.H. leg., primary lowland evergreen forest; Malaise trap; det. Rognes, K., 2012; BMSA-BECE 03118

• 1 ♀ 1 ♂, same collection data as previous; 0.70269'N, 24.20107'E, lowland evergreen swamp forest; BMSA-BECE ♀: 03372 DNA-COI F2, ♂: 03371 DNA-COI F5.

Equatorial Guinea • 1 ♀; Uelleburg. Benito Mts. (Spanish Guinea); 1–14 Feb. 1908; Tessmann, S.G. leg.; ZMHB Dipt S06219.

South Africa – KwaZulu-Natal • 1 ♀; Ramsgate Butterfly Sanctuary; 30°53.3'S, 30°20.4'E; 26–29 Apr. 2004; Mostovski, M. leg.; light trap; det. Thomas-Cabianca, A., 2018; NMSA DIP 84387.

Zimbabwe • 1 ♀; Bomponi, Vumba; 28 Jul. 1965; Cookson, D.M. leg.; det. Zumpt, F., 1969; NMSA DIP 019870.

Fainia inexpectata Zumpt, 1973

Figs 10–12, 13A, D, G

Fainia inexpectata Zumpt, 1973: 157
= *Fainia kirinyaga* Lehrer, 2007b: 2 syn. nov.

Type localities and repositories of primary types. *Fainia inexpectata*: Ivory Coast, Lamto, male(s) HT and PTs in MNHN (examined); Tanzania, Amani, male and female PTs in NMSA (examined). *Fainia kirinyaga*: Kenya, Nairobi, male HT in SMNHTAU (TAUI) 318989 (examined).

Distribution. Ivory Coast, Kenya, Malawi*, Tanzania (Zumpt 1973; Pont 1980; Lehrer 2007b).

Biology. Ecology, immature stages and life history unknown.

Redescription. A proper and complete description with male terminalia illustrations was given by Zumpt (1973). Here, we provide additional diagnostic characters, based on measurements and discuss the sternite 5 shape. Length 10.56 mm [10.14–11.13 mm] (n = 4). **Male** (n = 2). ***Head*** (Figs 10A and C). Eyes separated by 0.05 times width of head [0.04–0.05] (at narrowest point around 1.75 times the width of anterior ocellus); eye length 2.99 times height of gena [2.70–3.40]. Postpedicel length 2.28 times length of pedicel [2.09–2.52]. ***Terminalia*** (Figs 11, 12). Sternite 5 posteriorly formed by 3 lobes, 1 median and 2 outers (Figs 11F, 12F). Median lobe as Figs 11F, 12F and H, posterior margin triangular with a middle incision inwards, that could be slightly torn (Figs 11F, 12H) or not (Fig. 11F). Lateral lobes shorter than *F. elongata*, as in Fig. 9F. Surstylus and cercus as Fig. 11A, B. Phallus as in Fig. 11C–E, ventral plate in ventral view as in Fig. 11E; post- and pregonite as in Fig. 11G. **Female.** (n = 1). ***Head*** (Fig. 10B, D). Eyes separated by 0.20 times width of head; eye length 3.93 times height of gena. Postpedicel length 2.46 times pedicel length; fronto-orbital plate 0.70 as wide as frontal vitta at tip of ocellar triangle.

Figure 10. *Fainia inexpectata* Zumpt, 1973. General body views of male (MZSUR) and female (paratype NMSA DIP 61575) **A, C, E, G, I, J** male **A** head in frontal view **C** head in lateral view **E** abdomen in dorsal view **G** thorax in dorsal view **I** hind tibia with two anterodorsal setae (arrows) **J** lateral habitus and labels **B, D, F, H, K** female **B** head in frontal view **D** head in lateral view **F** abdomen in dorsal view **H** thorax in dorsal view **K** lateral habitus and labels. Scale bars: 2 mm.

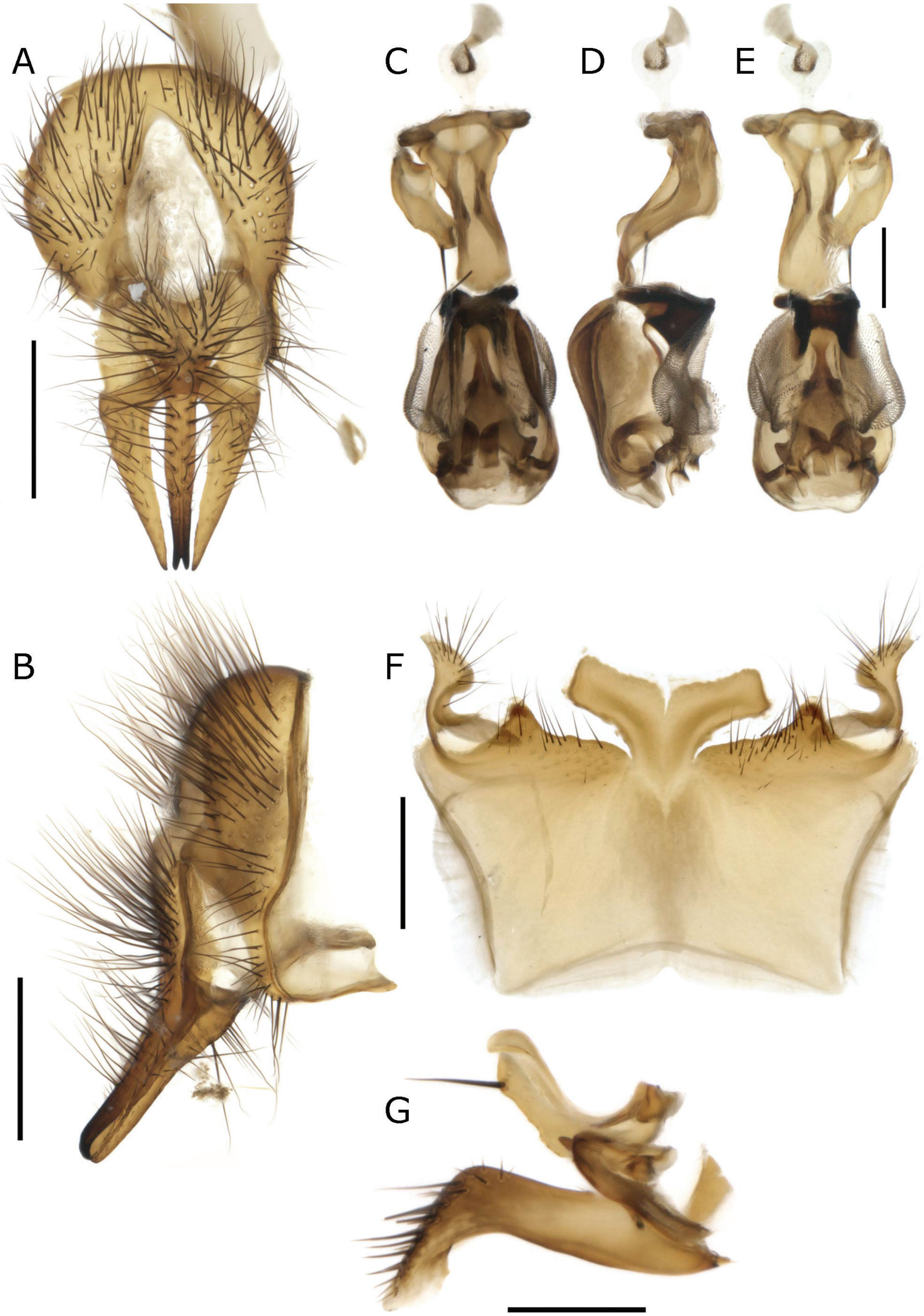

Figure 11. *Fainia inexpectata* Zumpt, 1973. Male terminalia (MZSUR) **A, B** epandrial complex in dorsal (**A**) and lateral (**B**) view **C–E** phallus in dorsal (**C**), lateral (**D**) and ventral (**E**) view **F** sternite 5 in ventral view and **G** postgonite (upper) and pregonite in lateral-internal view (**G**). Scale bars: 0.2 mm.

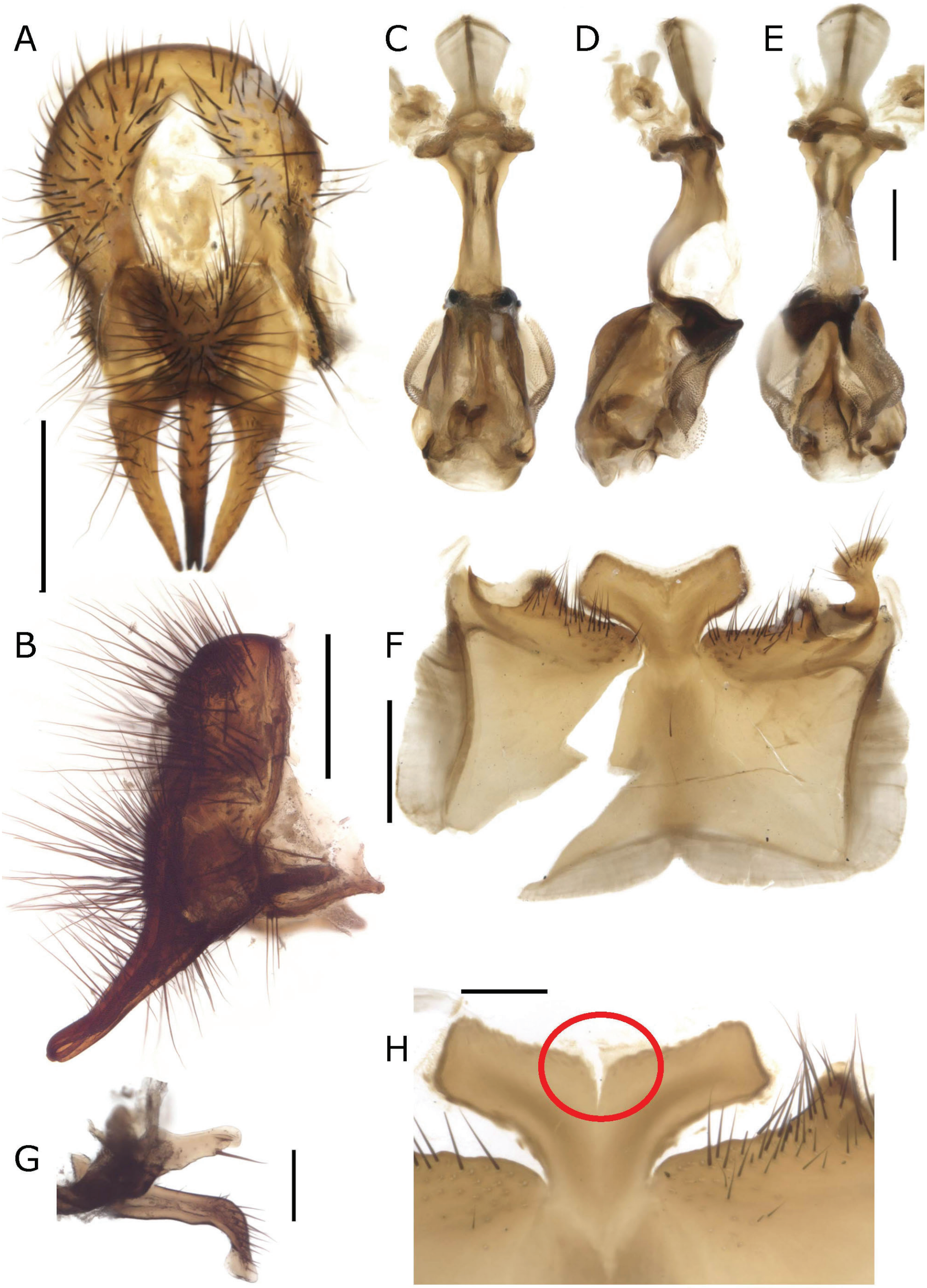

Figure 12. *Fainia kirinyaga* Lehrer, 2007b holotype (SMNHTAU (TAUI) 318989) male terminalia **A, B** epandrial complex in dorsal (**A**) and lateral (**B**) view **C–E** phallus in dorsal (**C**), lateral (**D**) and ventral (**E**) view **F** sternite 5 in ventral view and **G** postgonite (upper) and pregonite lateral-internal view (**G**) **H** *Fainia inexpectata* Zumpt, 1973 details of medial lobe tear (red circle) of the sternite 5 in ventral view. Scale bars: 0.2 mm.

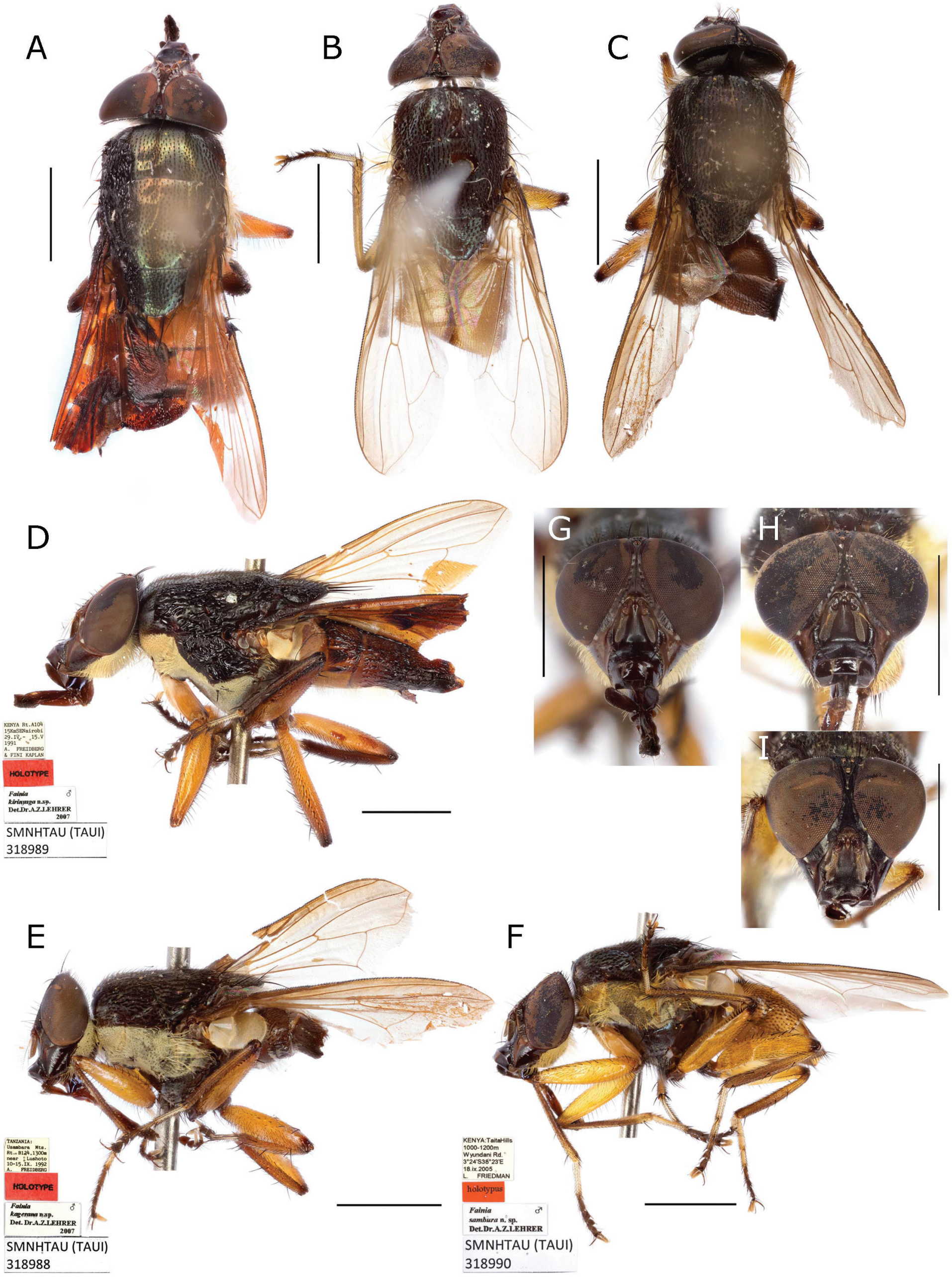

Figure 13. *Fainia kirinyaga* Lehrer, 2007b holotype (SMNHTAU (TAUI) 318989), *Fainia sambura* Lehrer, 2008 holotype (SMNHTAU (TAUI) 318989) and *Fainia kagerana* Lehrer, 2007a nom. nud. (SMNHTAU (TAUI) 318990) general body and heads views **A, D, G** *F. kirinyaga* dorsal habitus view (**A**), lateral habitus view (**D**) and head frontal view (**G**) **B, F, H** *Fainia sambura* dorsal habitus view (**B**), lateral habitus view (**F**) and head frontal view (**H**) **C, E, I** *Fainia kagerana* nom. nud. dorsal habitus view (**C**), lateral habitus view (**E**) and head frontal view (**I**). Scale bars: 2 mm.

Discussion. *Fainia inexpectata* is an uncommon Afrotropical species. The male terminalia were dissected by Zumpt and are preserved in a slide mounting preparation. The preserved terminalia are squashed and the structures overlap, so it was impossible to make a proper examination. Thus, the male terminalia structures were recognised and identified using a drawing provided by Zumpt (1973: fig. 4).

The description and drawings of *F. kirinyaga* syn. nov. (Lehrer 2011: 62–63) (Figs 12, 13A, D, G) match with *F. inexpectata.* After reviewing the HT of *F. kirinyaga* syn. nov., including the male terminalia (dissected by Lehrer and preserved in a microvial) (Fig. 12A–G), we conclude that the specimen belongs to *F. inexpectata*. We observed an apparent difference in the posterior area of the median lobe of sternite 5, which in *F. kirinyaga* syn. nov. (Fig. 12F) is continuous and, in *F. inexpectata* (Figs 11F, 12H and Zumpt 1973: fig. 4), apparently has a mid-ventral incision. After a careful examination under the microscope, we concluded that this incision is a tear in the structure since it is not surrounded by membrane (Fig. 12H).

Type material examined. *F. inexpectata* HT and PT: 4 ♂ Ivory Coast, Lamto / v. 1971, leg. D. Lachaise // det. Zumpt, 1973. At MNHN • *F. inexpectata* PT: 1 ♀ // PARATYPE // Amani, Tanganyika [= Tanzania] / leg. Paterson // det. Zumpt 1973 // NMSA DIP 61575 • *F. inexpectata* PT: 1 ♂ // PARATYPE // Amani, Tanganyika [= Tanzania] / leg. Paterson // Slide no 20 // det. Zumpt 1973 // NMSA DIP 61575 • *Fainia kirinyaga* HT: 1 ♂ KENYA Rt. A104 / 15 km SE Nairobi / 29.iv.-15.v / 1991 / A. FREIDBERG / & FINI KAPLAN // HOLOTYPE // n. sp / det. Dr A.Z. Lehrer / 2007 // SMNHTAU (TAUI) 318989.

Other material examined. 9 specimens (6 ♀♀ 3 ♂♂).

Kenya – Coast • 1 ♂; 10 km W. Malindi; UTM 37 M 615633 9643613; 100 m elev.; 24 May 2006; Cerretti, P., Avesani, D., Carpaneto, G. & Nardi, G. leg.; hand net; det. Rognes, K.; MZSUR, DNA-COI F6.

Malawi – Mulanje • 1 ♀; Mulanje mnt.; 15°56'10"S, 35°31'12"E; 1061 m elev.; 12–14 Nov. 2016; Kirk-Spriggs, A.H. & Muller, B. leg.; stream bed miombo woodland; Malaise traps; det. Thomas-Cabianca, A., 2019; BMSA (D) 92318.

Tanzania – Iringa • 1 ♀; Mufindi Dist. Uzungwa Scarp Forest Res.; 750 m elev.; 8–10 Mar. 1996; Mckamey, S. et al. leg.; ZMUC, Canopy light-trapping project; det. Rognes, K., 2013; ZMUC KR 001896, DNA-COI F19 – **Ludewa** • 1 ♀; Nyassa-See, Langenburg; Apr. 1899; Fülleborn, S. leg.; det. Thomas-Cabianca, A., 2019; ZMHB Dipt S06219 (previously determined as *F. albitarsis* by Enderlein, 1919; previously determined as *F. elongata* by Zumpt, 1953) • 1 ♀; Nyassa-See, Langenburg; 22 Nov.– 07 Dec. 1898; Fülleborn, S. leg.; det. Thomas-Cabianca, A., 2019; ZMHB Dipt S06219 (previously determined as *F. elongata* by Zumpt, 1953). – **Tanga** • 1 ♂; East Usambara, Amani, at Sigi River; 500 m elev.; 7 Feb. 1977; Enghoff, H., Lomholdt, O. & Martin O. leg.; det. Rognes, K., 2013; ZMUC 00516250 KR 001894, 00516251 KR 001895 • 2 ♀♀ 1 ♂; Tanga, Mkulumuzi, Gorge, Section No: VII, Tray No.: 8, Jar No. 19; 5–50 m elev.; Mar. 1992; Frontier-ZMUC leg.; det. Thomas-Cabianca, A., 2019; ZMUC.

Rhinia giriama **(Lehrer, 2007b) comb. nov.**

Fig. 14

≡ *Fainia giriama* Lehrer, 2007b: 3

Type locality and repository of primary types. *Fainia giriama*: Kenya, HT in SMNHTAU (TAUI) 318987 (examined).

Distribution. Kenya (Lehrer 2007b).

Biology. Ecology, immature stages and life history unknown.

Discussion. This is the only species described by Lehrer in *Fainia* that was based on a single female specimen. After examining the HT of *F. giriama* (Fig. 14), we conclude that it belongs to the genus *Rhinia*. The specimen is characterised by having wing cell r_{4+5} closed with a long petiole and apical area darkened, fore and mid first tarsomeres dark and palpi long, narrow and uniform in width, generally yellow (Fig. 14A, C). These characters fit the concept of the genus *Rhinia* (Zumpt 1958; Peris 1992) and not *Fainia* (see diagnosis above).

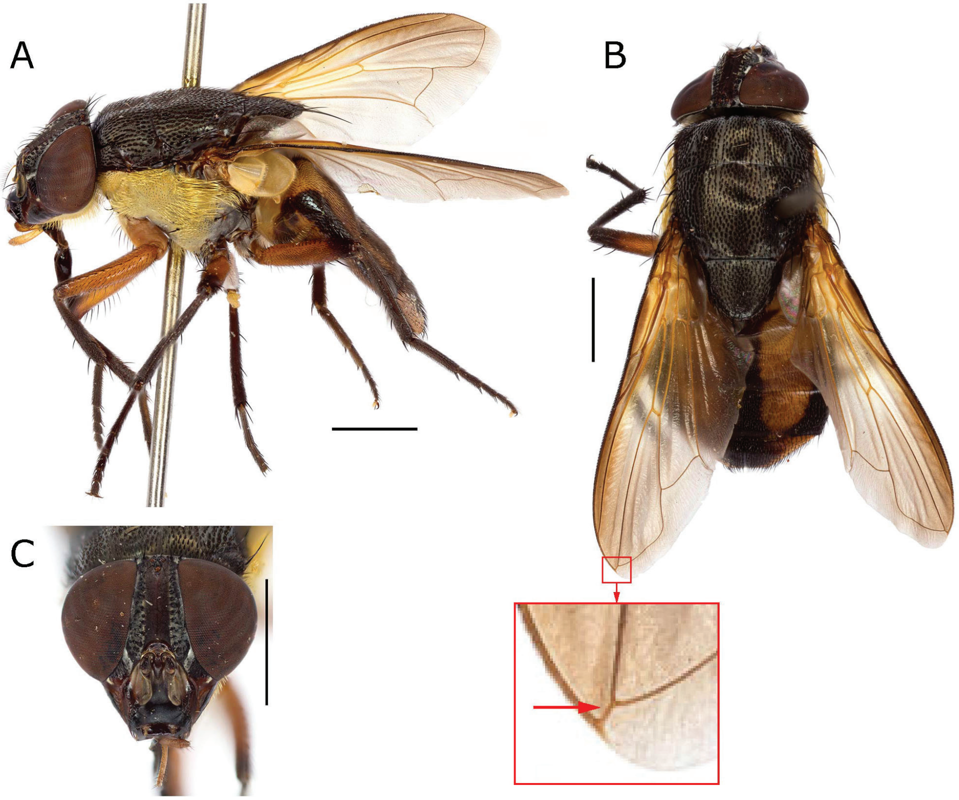

Figure 14. *Rhinia giriama* Lehrer, 2007b comb. nov. holotype (SMNHTAU (TAUI) 318987) general body and head views **A** lateral habitus view **B** dorsal habitus view and details of cell r_{4+5} showing long petiole (red square and arrow) and **C** head frontal view. Scale bars: 2 mm.

Type material examined. *Fainia giriama* HT: 1 ♀ KENYA Tambach / 40 km E Eldoret / 12.v.1991 / A. FREIDBERG / & FINI KAPLAN // HOLOTYPE // *Fainia* / *giriama* n. sp / det. Dr A. Z. Lehrer / 2007 // SMNHTAU (TAUI) 318987.

Notes on Rhiniidae classification and potential apomorphies for Rhiniinae

Brauer and von Bergenstamm (1889) split rhiniids into Cosminidae, Rhininiidae and Rhyncomyiidae. Riley and Johansen (1915) then reclassified them as subfamilies (Cosmininae, Rhininiinae and Rhyncomyiinae) within Calliphoridae. Malloch (1926) classified all rhiniids in Rhiniinae (within Calliphoridae), split into two tribes, based on the proepisternal seta, present in Cosminini and absent in Rhiniini. Malloch's classification was also followed by Senior-White et al. (1940), but Peris (1952) discarded it, arguing that some species of *Stegemosa* Loew (Cosmininae) lack a proepisternal seta, while some species of *Chlororhina* Townsend (Rhiniinae) present it. Other authors classified Rhiniinae (within Calliphoridae) without using tribes or subfamilies, because of the lack of diagnostic characters and morphological studies (Dear 1977; James 1977; Rognes 1998) or because they considered the subdivisions unnecessary for a higher taxon with so few genera (Peris 1952, 1992). Lehrer (1970) proposed a radical approach, dividing Rhiniinae (within Calliphoridae) into six tribes, based on the morphology of the male terminalia (Isomyiini, Rhiniini, Rhyncomyiini, Stegosomini, Sokotrini and Trychoberiini) and, years later, split rhiniids into three subfamilies: Fainiinae, Rhiniinae and Stomorhiniinae (sic) (Lehrer 2011).

More recently, in addition to the traditional characters used to split the two primary lineages of Rhiniidae (Peris 1952; Zumpt 1958; Kurahashi and Kirk-Spriggs 2006), Fang and Fan (1988) incorporated characters of the phallus. In Cosmininae, the acrophallus is often connected with the base of the hypophallus (= mid-ventral wall) and the epiphallus is developed, while in Rhiniinae, the acrophallus stretches out from the paraphallus and the epiphallus is undeveloped.

Recent molecular evidence, based on DNA Ultra Conserved Element (UCE) sequence data, reconstructed three major clades within Rhiniidae, with Cosmininae split into two clades (one containing the exclusive Oriental genus *Sumatria* and the other, the rest of the Cosmininae genera) and Rhiniinae monophyletic (Buenaventura et al. 2020). In our examination of all of the Afrotropical rhiniids, two morphological characters in the phallus support potential synapomorphies for the Rhiniinae (Table 1). First, the absence of an epiphallus is apomorphic in Rhiniinae, as was also suggested by Fang and Fan (1988) and the epiphallus is present (pleisomorphic state) in other

Table 1. Proposed apomorphies (in bold) for Rhiniinae, polarised using the character state found in Bengaliinae (Diptera: Calliphoridae) (Rognes 2009) and Afrotropical Cosmininae (Buenaventura et al. 2020).

Character	**Character state**		
	Bengaliinae	Cosmininae	Rhiniinae
Epiphalus	present	present	**absent**
Basi- and distiphallus	fused	fused	**not fused, connected by desclerotised membrane, giving independent mobility to these structures**

Rhiniidae and its sister group Bengaliinae (Calliphoridae) (Rognes 2009; Cerretti et al. 2019; Kutty et al. 2019; Buenaventura et al. 2020). Second, the basi- and distiphallus are connected by a desclerotised membrane, which is apomorphic in Rhiniinae, whereas they are plesiomorphically fused in other Rhiniidae and Bengaliinae (Rognes 2009).

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RESEARCH ARTICLE

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Revision of Korean species of the genus *Batriscenellus* Jeannel (Staphylinidae, Pselaphinae, Batrisitae) with description of one new species

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Abstract

The genus *Batriscenellus* Jeannel, 1958 (type species: *Batrisus fragilis* Sharp) includes 35 species and is known from South Korea, China, Japan, Russia, and India. Three species, *B. vicarius*, *B. auritus*, and *B. orientalis* have been documented from the Korean Peninsula. One additional species, *Batriscenellus koreanus* **sp. nov.**, is described as new. Redescriptions of the Korean species, a species key, illustration of habitus, and diagnostic characters are provided.

Keywords

Batrisini, biodiversity, biogeography, rove beetles, systematics, taxonomy

Introduction

The genus *Batriscenellus* Jeannel, 1958 was described based on *Batrisus fragilis* Sharp from Kioto, Japan. It includes 35 species and is known from South Korea, China, Japan, Russia, and India (Yin 2020). Three species, *B. vicarius* Löbl, 1973, *B. orientalis* (Löbl, 1973), and *B. auritus* (Löbl, 1974) are known from the Korean Peninsula. The first Korean species of the genus, *Batriscenellus japonicus vicarius* Löbl, 1973 was described from the northern part of the Korean Peninsula. It was subsequently raised to the species level by Nomura and Lee (1992). Löbl (1973, 1974) described two additional species, *Batrisiella aurita* and *Batrisiella orientalis*, also from the northern part of the Korean Peninsula, and they were transferred to *Batriscenellus* by Yin et al. (2011) and Nomura (1991), respectively.

During a revisionary study of the Korean *Batriscenellus* species, we documented four species, the previously known three species and one new species. The present paper presents the first revisionary study of Korean species of *Batriscenellus*, and describes the new species. This new species brings the number of *Batriscenellus* species from the Korean Peninsula to four.

Materials and methods

Twenty-two specimens were examined. They are deposited in the following collections:

CBNUIC	Chungbuk National University Insect Collection, Cheongju, Republic of Korea;
CNUIC	Chungnam National University Insect Collection, Daejeon, Republic of Korea;
NIBR	National Institute of Biological Resources, Incheon, Republic of Korea.

At least one specimen of each species was dissected to study male genitalia and other detailed characters. Terminology and nomenclature using descriptions follow Chandler (2001). Numbering of abdominal sclerites indicates a morphological segment. Specimen label data for the holotypes is transcribed verbatim. Data for the other specimens are standardized for consistency. Application of the terms 'dorsal' and 'lateral' to the male genitalia including the right and left apical lobe and the paramere refer to the orientation in the illustrations. The specimens were observed using a Leica M80 and MD 1000 LED optical microscope and images generated using Leica Las version 4.12 and Zerene Stacker. The map of South Korea is based on an image from SimpleMappr (Shorthouse 2010) that was subsequently modified to add locality marks.

Key to Korean species of the genus *Batriscenellus* Jeannel

1 Abdominal tergite IV or VI without depression; phallobase of male genitalia without apophysis (Fig. 8) .... ***Batriscenellus orientalis***

– Abdominal tergite with depression (Figs 1D, 3C, 5C); left side of phallobase of male genitalia with apophysis posteriorly (Figs 2A, B, 4A, B, 6A, B)....... **2**

2 Elytra IV or VI with a pair of processes laterally; abdominal tergite IV with sulcus (Fig. 5C); abdominal ventrite VIII without paired medial setiferous patches (Fig. 5D) .... ***B. auritus***

– Elytra without processes; abdominal tergite VI with sulcus (Figs 1D, 3C); abdominal ventrite VIII with a pair of medial setiferous patches (Figs 1E, 3D).... **3**

3 Abdominal ventrites IV–VII with a pair of long setae at middle (Fig. 3D); paramere of male genitalia not bifid (Fig. 4C, D)........................***B. vicarius***

– Abdominal ventrites IV–VII without a pair of long setae at middle (Fig. 1E); paramere of male genitalia bifid (Fig. 2C, D) .... ***Batriscenellus koreanus* sp. nov.**

Systematics

Family Staphylinidae Latreille, 1802
Subfamily Pselaphinae Latreille, 1802
Supertribe Batrisitae Reitter, 1882

Batriscenellus Jeannel, 1958 (type species: *Batrisus fragilis* Sharp, 1883)

Batriscenellus Jeannel, 1958 (type species: *Batrisus fragilis* Sharp, 1883)
Batriscenellus Jeannel, 1958: 60. Löbl and Besuchet 2004: 276. Yin et al. 2011: 37.
Batriscenellinus Nomura, 1991: 321 (type species *Batriscenellus uenoi* Nomura, 1991).
Coreoscenellus Nomura & Lee, 1993: 12 (type species *Batriscenellus brachygaster* Nomura & Lee, 1993).
Nipponoscenellus Nomura, 1991: 310 (type species *Batriscenellus transformis* Nomura, 1991).
Scaioscenells Jeannel, 1958: 60 (type species *Batrisus similis* Sharp, 1883).

Diagnosis. Members of this genus are easily separated from other genera of Batrisitae by the following combination of characters: head triangular with the transverse sulcus dorsally at mid-level of head and vertexal foveae; antennomere 1 subquadrate with dense trichomes (Figs 1C, 3B, 5B, 7B), antennomeres 9–11 clubbed; pronotum with median antebasal fovea, lateral antebasal foveae, inner basolateral foveae and outer basolateral foveae, disc with median and lateral longitudinal sulci; elytra with two basal foveae; mesotibia with spine on distal margin (Fig. 1B); abdomen rounded laterally; abdominal tergite IV largest; male genitalia asymmetric (Figs 2, 4, 6, 8); paramere singular and originating from ventral phallobase.

Distribution. South Korea, Russia (Far East), Japan, China.

Batriscenellus koreanus Kang, Park, Kim & Park, sp. nov.

http://zoobank.org/6E280D51-FC3F-4AE7-9A2C-9AAF2132BC74
Figs 1, 2

Material examined. ***Holotype.*** 1♂ (NIBR), "Korea: Chungbuk prov. / Cheongwon-gun, / Bugi-myeon, Hwasang-ri, / 12III2020, 36°44'08.00"N, 127°29'01.40"E, 38 m / sifting soil litter / M-S Jang, / T-Y Jang". ***Paratype*** (1 male). 1♂ (CBNUIC), same data as holotype.

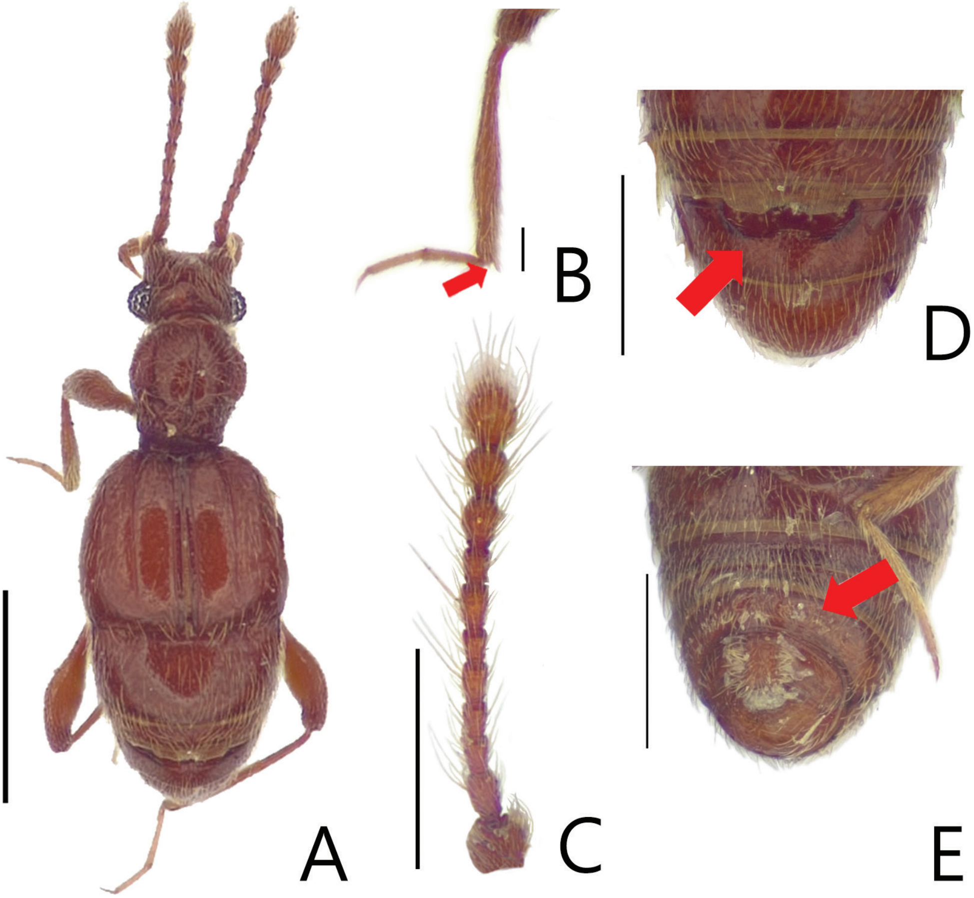

Figure 1. Habitus figures of *Batriscenellus koreanus* sp. nov. **A** dorsal view **B** mesotibia **C** antennae **D** dorsal view of abdomen **E** ventral view of abdomen. Scale bars: 1 mm (**A**); 0.5 mm (**B–D**).

Diagnosis. This species can be distinguished from the other *Batriscenellus* species by the following combination of characters: antennomere 8 subquadrate and smallest (Fig. 1C), abdominal tergite V with a pair of median setiferous patches, VI with deep mediobasal sulcus (Fig. 1D), abdominal ventrite VIII with depressionand pair of dense setiferous patches (Fig. 1E), phallobase of male genitalia widely expanded, apical lobe of male genitalia curved to right in lateral view (Fig. 2C, D), paramere forked into two branches in lateral view, major branch curved to right (Fig. 2C, D).

Description. Length 2.03–2.15 mm. Body reddish-brown (Fig. 1A). ***Head.*** All antennomeres with tubercles and long setae (Fig. 1C). Antennomere 1 subquadrate with dense trichomes on lateral margin, 2–7 rectangular, 8 rectangular [from photo] and smallest, 9 rectangular and larger than 3–8, 10 rhombic, 11 oval. ***Thorax.*** Each elytron with shallow discal stria. ***Abdomen.*** Abdominal tergite V with pair of setiferous patches, VI with deep sulcus (Fig. 1D: arrow). Abdominal ventrite VIII with depression and pair of dense setiferous patches (Fig. 1E: arrow). ***Aedeagus.*** Left side of phal-

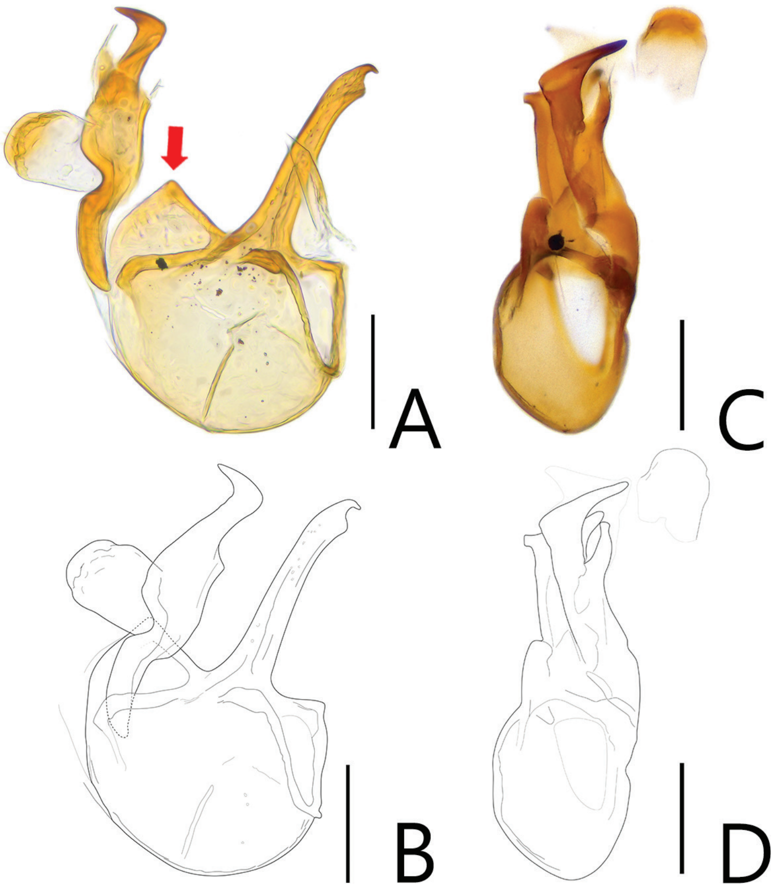

Figure 2. Aedeagi of *Batriscenellus koreanus* sp. nov. **A, B** dorsal view **C, D** lateral view. Scale bars: 0.1 mm.

lobase widely expanded in dorsal view (Fig. 2A, B: arrow). Apical lobe of male genitalia curved right in lateral view (Fig. 2C, D). Paramere forked into two branches in lateral view, major branch curved to right (Fig. 2C, D).

Distribution. South Korea (Fig. 9: square)

Etymology. This species is named for Korea, where this species was collected.

Habitat. The two specimens of this species were collected by sifting soil litter of a riverside grassland.

Batriscenellus vicarius **Löbl, 1973**

Figs 3, 4

Batriscenellus japonicus vicarius Löbl, 1973: 322. Nomura 1991: 301.

Batriscenellus vicarius: Nomura 1992: 61. Cho and Ahn 2001: 53. Park et al. 2013: 123. Löbl and Besuchet 2004: 276. Schülke and Smetana 2015: 367.

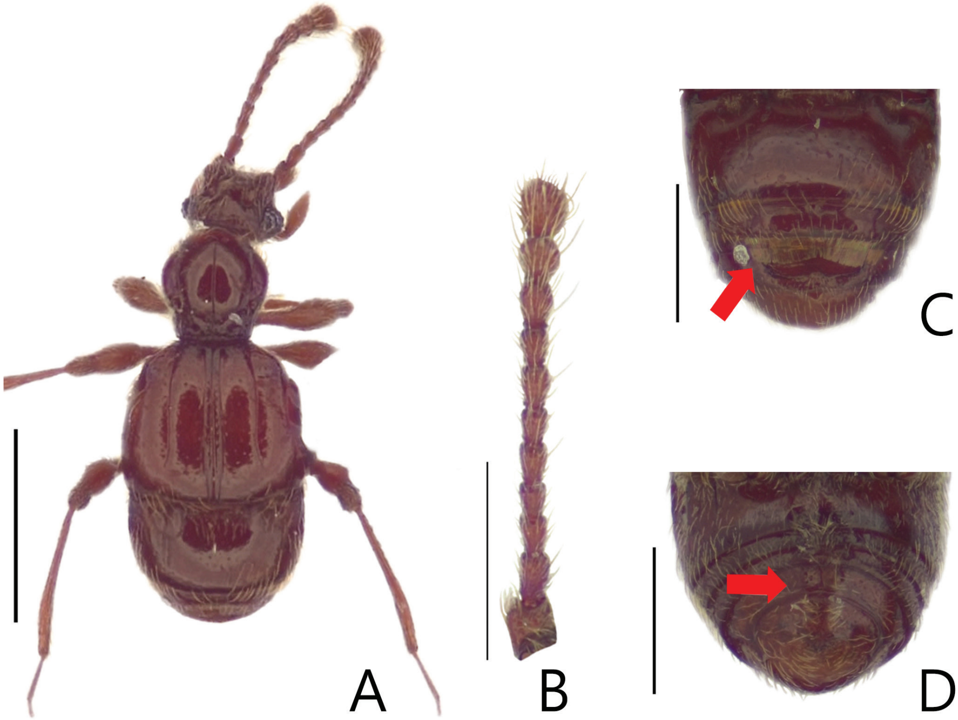

Figure 3. Habitus figures of *Batriscenellus vicarius* **A** dorsal view **B** antennae **C** dorsal view of abdomen **D** ventral view of abdomen. Scale bars: 1 mm (**A**); 0.5 mm (**B–D**).

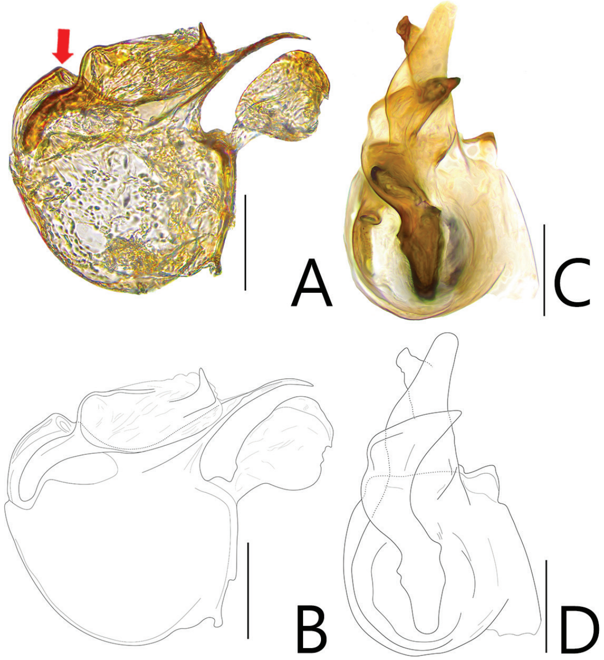

Figure 4. Aedeagi of *Batriscenellus vicarius* **A, B** dorsal view **C, D** lateral view. Scale bars: 0.1 mm.

Material examined. 1♂ (CBNUIC), Chungbuk Prov., Cheongwon-gun, Bugi-myeon, Hwasang-ri, 38 m, 36°44'08.00"N, 127°29'01.40"E, 12 III 2020, M-S Jang, T-Y Jang, sifting soil litter; 1♂1♀ (1♂ aedeagus dissected and mounted in Euparal on clear plastic card, CBNUIC), Gyeonggi Prov., Baekdun-ri, Mt. 15–35, Buk-myeon, Gapyeong-gun, 509 m, 37°55'10.50"N, 127°26'21.80"E, 13 X 2019, J-Y Kang, J-W Kim, sifting leaf & soil litter; 1♀ (CBNUIC), Gyeonggi Prov., Baekdunro-gil 650, Buk-myeon, Gapyeong-gun, 503 m, 37°55'09.80"N, 127°26'22.50"E, 13 X 2019, M-H Song, U-J Byeon, sifting leaf & soil litter; 1♀ (CBNUIC), Gyeonggi Prov., Baekdun-ri, Buk-myeon, Gapyeong-gun, 440 m, 37°54'57.40"N, 127°26'17.20"E, 13 X 2019, J-W Kang, M-H Song, U-J Byeon, T-Y Jang, sifting leaf & soil litter; 1♂ (CBNUIC), Chungbuk Prov., Danyang-gun, Danyang-eup, Yangbangsan-gil, 585 m, 36°58'14.20"N, 128°22'57.60"E, 12 III 2020, M-S Jang, J-W Kim, sifting leaf & soil litter.

Diagnosis. This species can be distinguished from the other *Batriscenellus* species by the following combination of characters: antennomeres 2–8 rectangular (Fig. 3B); abdominal tergite V with pair of basolateral setiferous patches, VI with deep sulcus (Fig. 3C: arrow); abdominal ventrites IV–VII with pair of long setae at middle (Fig. 3D), VIII with carina and pair of dense medial setiferous patches (Fig. 3D: arrow); left side of phallobase of male genitalia widely expanded in dorsal view (Fig. 4A, B: arrow); paramere of male genitalia curved to left in dorsal view (Fig. 4A, B).

Description. Length 1.85–2.02 mm. Body reddish-brown (Fig. 3A). ***Head.*** All antennomeres with tubercles and long setae (Fig. 3B). Antennomere 1 subquadrate with dense trichomes laterally 2–8 rectangular, 9 rectangular and larger than 2–8, 10 rhombic, 11 oval. ***Thorax.*** Pronotum with medial and lateral longitudinal sulci. Mesoventrite with lateral setiferous patches. Each elytron with shallow discal stria. ***Abdomen.*** Abdominal ventrites IV–VII with pair of long setae distinct located at middle, distinct in female (Fig. 3D: arrow), IV with setiferous patches at posterior margin of coxal cavity of hind leg (Fig. 3D). ***Aedeagus.*** Left side of phallobase of male genitalia widely expanded in dorsal view (Fig. 4A, B: arrow). Paramere of male genitalia curved to left in dorsal view (Fig. 4A, B).

Distribution. South Korea (Fig. 9: circle), Russia (Far East), Japan, China.

Habitat. Specimens of this species were collected by sifting soil or leaf litter.

Batriscenellus auritus (Löbl, 1974)

Figs 5, 6

Batrisiella aurita Löbl, 1974: 92. Nomura and Lee 1993: 46. Kim et al. 1994: 144. Cho and Ahn 2001: 53. Löbl and Besuchet 2004: 277.

Batriscenellus auritus: Yin et al. 2011: 37. Park et al. 2013: 123. Schülke and Smetana 2015: 366.

Material examined. 1♂ (1♂ aedeagus dissected and mounted in Euparal on clear plastic card, CNUIC), Chungnam Prov., Gongju City, Mt. Gyeryongsan, Geumsubong, 23 VI 2000, H.-J. Kim, ex near stream.

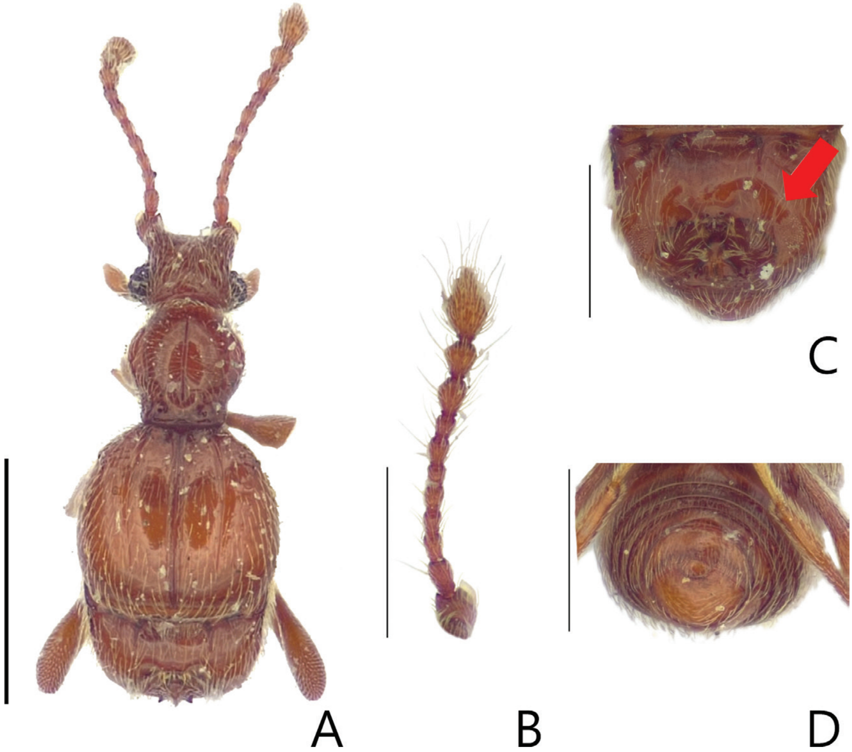

Figure 5. Habitus figures of *Batriscenellus auritus* **A** dorsal view **B** antennae **C** dorsal view of abdomen **D** ventral view of abdomen. Scale bars: 1 mm (**A**), 0.5 mm (**B–D**).

Diagnosis. This species can be distinguished from the other *Batriscenellus* species by the following combination of characters: antennomere 1 subquadrate with dense yellowish trichomes on lateral margin; elytra with pair of process antero-laterally; abdominal tergite IV with deep mediobasal sulcus (Fig. 5C); abdominal ventrite IV with dorsolateral setiferous patches; paramere of male genitalia forked into two branches, right paramere curved to right in dorsal view (Fig. 6A, B).

Description. Length 1.85 mm. Body reddish-brown (Fig. 5A). ***Head.*** All antennomeres with tubercles and long setae (Fig. 5B). Antennomere 1 subquadrate with dense yellowish trichomes on lateral margin, 2–7 rectangular, 8 subquadrate and smallest, 9–10 rhombic, 11 oval. ***Thorax.*** Mesoventrite with lateral setiferous patches. Elytra with lateral process. ***Abdomen.*** Abdominal tergite IV with deep sulcus (Fig. 5C: arrow). Abdominal ventrite IV with pair of dorsolateral setiferous patches. ***Aedeagus.*** Apical lobe of male genitalia curved to right and expanded apical margin in dorsal view (Fig. 6A, B). Two branches of paramere curved to right in lateral view (Fig. 6C, D).

Comments. The basal bulb of the male genitalia are broken in Figure 6D. See Löbl (1974: 93) for other examples of the aedeagus.

Distribution. South Korea (Fig. 9: triangle).

Habitat. A single specimen of this species was collected near a stream.

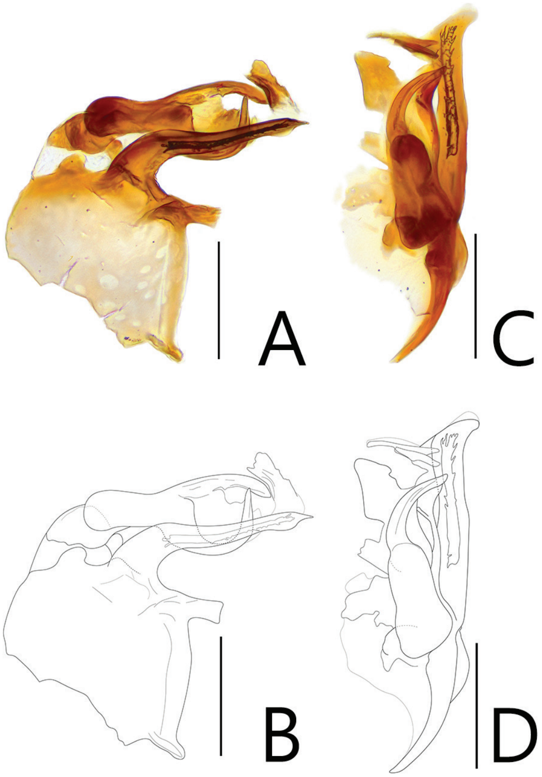

Figure 6. Aedeagi of *Batriscenellus auritus* **A, B** dorsal view **C, D** lateral view. Scale bars: 0.1 mm.

***Batriscenellus orientalis* (Löbl, 1973)**
Figs 7, 8

Batrisiella orientalis Löbl, 1973: 322.
Batriscenellus orientalis: Nomura 1991: 317. Kim et al. 1994: 144. Cho and Ahn 2001: 53. Löbl and Besuchet 2004: 276. Shao et al. 2010: 67. Yin et al. 2011: 37. Park et al. 2013: 123. Schülke and Smetana 2015: 366.
Batriscenellus (*Coresoscenellus*) *brachygaster* Nomura & Lee, 1993: 13. Nomura 2005: 214.

Material examined. 3♂♂ (1♂, aedeagus dissected and mounted in Euparal on clear plastic card, CBNUIC), Gangwon Prov., Jungyeong-gil, Miro-myeon, Samcheok-si, 69 m, 37°22'02.80"N, 129°05'06.60"E, 22 VIII 2018, Y-J Choi, light trap; 1♂ (CBNUIC), Chungbuk Prov., Jecheon-si, Hansu-myeon, Songgye-ri, 258 m, 36°52'53.40"N, 128°05'06.80"E, 23 V 2019, Y-J Choi, sifting litter near stream; 1♀ (CBNUIC), Chungbuk Prov., Mt. Worak, Mireuksonggye-ro, Hansu-myeon, Jecheon-si, 220 m, 36°52'07.60"N, 128°05'10.80"E, 14 VI 2018, Y-J Choi, sifting litter; 1♂ (CBNUIC), Gyeongbuk Prov., Uljin-gun, Onjeong-myeon, Woeseonmi-ri, 592 m, 36°45'28.30"N, 129°18'05.30"E, 9 VIII 2018, J-W Kang, sifting leaf litter;

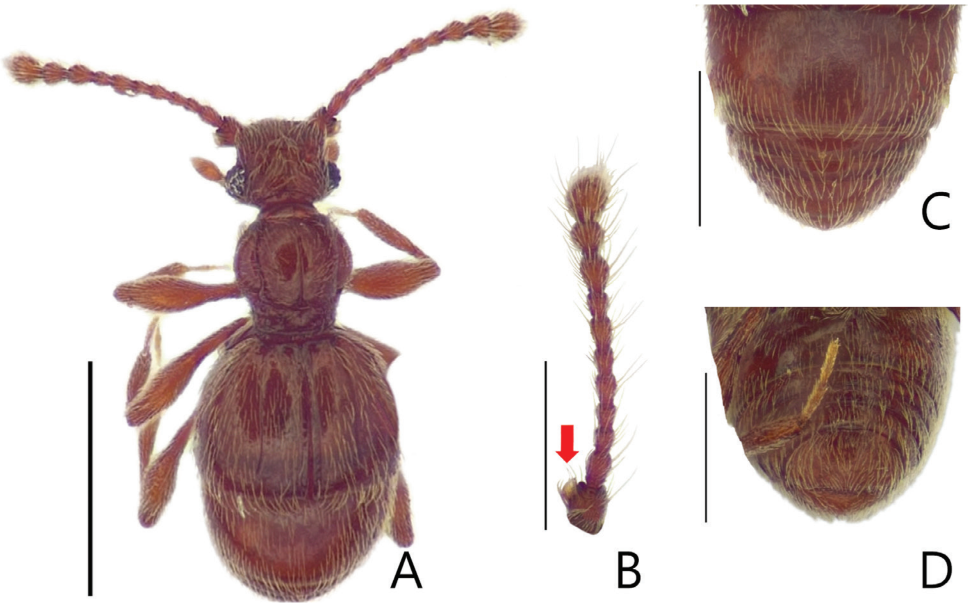

Figure 7. Habitus figures of *Batriscenellus orientalis* **A** dorsal view **B** antennae **C** dorsal view of abdomen **D** ventral view of abdomen. Scale bars: 1 mm (**A**), 0.5 mm (**B–D**).

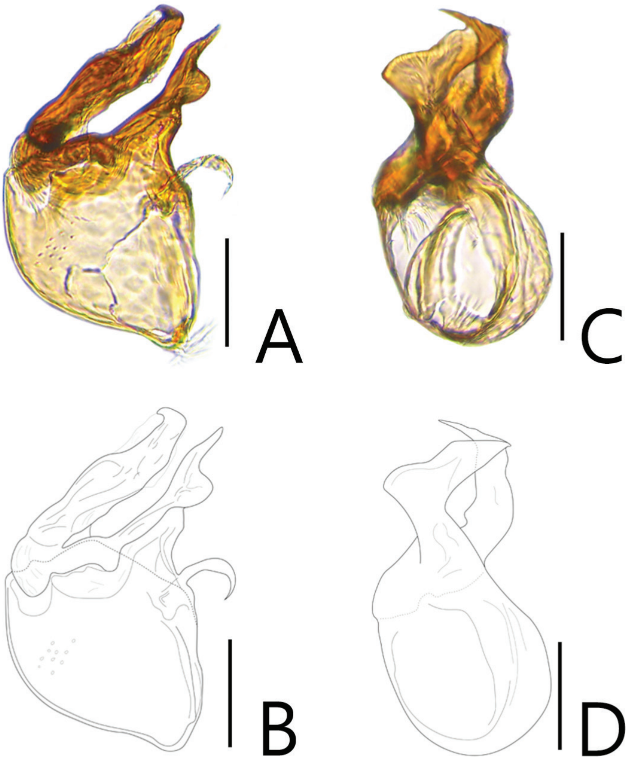

Figure 8. Aedeagi of *Batriscenellus orientalis* **A, B** dorsal view **C, D** lateral view. Scale bars: 0.1 mm.

Figure 9. Collection localities of *Batriscenellus koreanus* sp. nov.: square; *B. vicarius*: circle; *B. auritus*: triangle; *B. orientalis*: diamond.

1♂ (CBNUIC), Gyeongbuk Prov., Mungyeong-si, Sanyang-myeon, Sinjeon-ri, 74 m, 36°36'16.00"N, 128°15'47.00"E, 9 V 2019, U-J Byeon, M-H Song, sifting leaf litter; 2♀♀ (CBNUIC), Jeonnam Prov., Haenam-gun, Gyegok-myeon, Dangsan-ri, 211 m, 34°40'53.00"N, 126°38'56.00"E, 18 V 2019, J-S Park, M-H Song, leaf litter & dead wood debris; 1♀ (CBNUIC), Gyeongbuk Prov., Yeongju-si, Munsu-myeon, Wolho-ri, 172 m, 36°45'45.61"N, 128°37'25.73"E, 4 V 2019, M-S Jang, sifting leaf litter; 1♀ (CBNUIC), Gyeongbuk Prov., Yecheon-gun, Yongmun-myeon, Sanggeumgok-ri, 220 m, 36°41'51.00"N, 128°24'18.00"E, 5 V 2019, U-J Byeon, sifting leaf litter; 1♀ (CBNUIC), Gyeongbuk Prov., Yecheon-gun, Yongmun-myeon, Nosa-ri, 246 m, 36°40'57.00"N, 128°22'31.00"E, 19 VII 2019, U-J Byeon, sifting leaf & soil litter.

Diagnosis. This species can be distinguished from the other *Batriscenellus* species by the following combination of characters: antennomere 1 subquadrate with dense yellowish trichomes; elytra with lateral process; right margin of apical lobe of male genitalia expanded in dorsal view (Fig. 8A, B); paramere of male genitalia curved to left in dorsal and lateral views (Fig. 8C, D).

Description. Length 1.71–2.09 mm. Body reddish-brown (Fig. 7A). ***Head.*** All antennomeres with tubercles and long setae (Fig. 7B). Antennomere 1 subquadrate with dense yellowish trichomes on lateral margin (Fig. 7B: arrow), 2–7 rectangular, 8 subquadrate and smallest, 9 rhombic, 10 subquadrate, 11 oval. ***Thorax.*** Mesoventrite with pair of lateral setiferous patches. Each elytron with one discal stria. ***Abdomen.*** Abdominal tergite IV expanded (Fig. 5C). Abdominal ventrite IV with lateral setiferous patches.

Distribution. South Korea (Fig. 9: diamond), Japan, China.

Habitat. Most specimens of this species were collected by sifting leaf litter or dead wood debris. One specimen was captured by a light trap.

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RESEARCH ARTICLE

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A new species of *Hemiptarsenus* Westwood (Hymenoptera, Eulophidae) from China, with a key to Chinese species

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Abstract

A new species, *Hemiptarsenus jilinus* Tao, **sp. nov.**, is described and illustrated. All the type specimens were reared from *Chromatomyia horticola* (Goureau) (Diptera: Agromyzidae), a leafminer attacking the plants *Ixeris polycephala* Cass. and *Pterocypsela indica* (L.) Shih, in Jilin Province, north-eastern China. A key to Chinese species of the genus is provided.

Keywords

Agromyzidae, Chalcidoidea, *Chromatomyia horticola*, Eulophinae, parasitoids, taxonomy

Introduction

Hemiptarsenus Westwood, 1833 (Hymenoptera: Eulophidae) contains 33 valid species worldwide (Noyes 2020), including seven species known from China (Sheng et al. 1989; Lee 1990; Zhu et al. 2000; Xu et al. 2001; Zhu and Huang 2002; Yang et al. 2015).

Leaf miners are serious pests of crops and ornamental plants worldwide (Spencer 1973). Parasitoids play an important role in inhibiting the occurrence of leaf miners (Gratton and Welter 2001). *Hemiptarsenus* includes numerous species which are potentially important for biological control of leaf miners belonging to Diptera, Lepidoptera, Coleoptera and Hymenoptera (Gibson 1997; Burgio et al. 2007; Yang et al. 2015).

Significant contributions to the taxonomy of this genus have been made by several authors, such as Bouček's (1959) and Zhu and Huang's (2003) studies for the Central European countries, Shafee and Rizvi's (1988) and Narendran's (2011) studies for the Indian fauna, Zhu et al.'s (2000) study for the Chinese fauna. In systematic studies at the generic level, Girault (1924) synonymised *Neodimmockia* Dodd, 1917 and *Hemiptarsenoideus* Girault, 1916; Schauff and LaSalle (1993) synonymised *Notanisomorpha* Ashmead, 1904; Bouček (1988) synonymised *Eriglyptoideus* Girault, 1913; Burks (2012) synonymised *Cleolophus* Mercet, 1924 and *Parpholema* Szelenyi, 1981 with the genus *Hemiptarsenus*.

In the present paper, a new species, which was reared from *Chromatomyia horticola* (Goureau) (Diptera: Agromyzidae), is described and a key to the known Chinese species of *Hemiptarsenus* is given.

Materials and methods

All the specimens were reared from *Chromatomyia horticola* on rolled leaves of *Ixeris polycephala* Cass. (Campanulales: Compositae) and *Pterocypsela indica* (L.) Shih (Asterales: Asteraceae) from Jingyuetan National Forest Park of Changchun City, Jilin Province of China. Different host plants were placed in different insect cages, and each cage was labeled with the collecting date, locality, and host plant. The plants were maintained at 24–26 °C until emergence.

Photographs of the wings were taken with an OLYMPUS SZX16 stereomicroscope. Other photographs were taken with a KEYENCE VHX–2000 digital microscope. The type material of the new species was deposited in the Insect Museum of Jilin Agricultural University (**IMJAU**), Changchun, China.

The morphological terminology follows Yoder et al. (2010), Gibson (1997) and Bouček (1988) and the following abbreviations are used: F1–4, flagellar segments 1–4; SMV, submarginal vein; MV, marginal vein; PMV, postmarginal vein; STV, stigmal vein; POL, minimum distance between posterior ocelli; OOL, minimum distance between a posterior ocellus and corresponding eye margin. Absolute measurements in millimeters (mm) were used for the body and fore wing lengths. For all other dimensions, relative measurements were used.

Taxonomy

Hemiptarsenus Westwood, 1833

Hemiptarsenus Westwood, 1833: 122–123. Type-species: *Hemiptarsenus fulvicollis* Westwood

Diagnosis. Torulus high on head, above lower margin of eye, hence apex of scape extending above level of vertex; funicle 4-segmented in female, and with 3 branches in male; notauli incomplete; axillae not angulately advanced; scutellum without sublateral grooves; median carina and plicae on propodeum nearly always indistinct or absent in majority of species; petiole distinct though not very long; fore wing and costal cell long and narrow, the fore wing at least 2.6 times as long as wide and costal cell 10–15 times as long as wide.

Key to species of *Hemiptarsenus* Westwood from China (females)

1 Propodeum elevated medially; plicae and median carina at least partly distinct **2**
– Propodeum sloping laterally; plicae or median carina absent **5**
2 Propodeum less than half length of scutellum; mesosoma yellow with pronotum, mid lobe of mesoscutum, dorsellum, and median area between plicae and median carina dark .... ***H. strigiscuta*** **Zhu, LaSalle & Huang**
– Propodeum about as long as scutellum; mesosoma completely green **3**
3 Scutellum longitudinally sculptured; legs yellow with coxae and trochanters white .... ***H. jilinus*** **Tao, sp. nov.**
– Scutellum reticulate; legs completely yellow **4**
4 Petiole at least as long as wide; metafemora dark .... ***H. unguicellus*** **(Zetterstedt)**
– Petiole short, transverse; metafemora yellow .... ***H. tabulaeformisi*** **Yang**
5 PMV shorter than or at most as long as STV, fore wing with disc slightly clouded .... ***H. fulvicollis*** **Westwood**
– PMV 2× length of STV, fore wing hyaline **6**
6 Scutellum reticulate; mesoscutum with transverse, yellow patch .... ***H. zilahisebessi*** **Erdös**
– Scutellum longitudinally sculptured; mesoscutum completely metallic green 7
7 Mesosoma with scutellum orange-yellow or yellow .... ***H. ornatus*** **(Nees)**
– Mesosoma completely metallic green .... ***H. varicornis*** **(Girault)**

Hemiptarsenus jilinus Tao, sp. nov.

http://zoobank.org/4D489171-EEA6-4DA1-9F40-02F7E9F996F3
Figs 1–10

Material examined. ***Holotype*** ♀ (IMJAU), China: Jilin Province, Jingyuetan National Forest Park of Changchun City (43°79.32'N, 125°45.23'E), 3–9 July 2019, reared by Rui-Jie Wang from *Chromatomyia horticola* (Goureau) (Diptera: Agromyzidae) on rolled leaves of *Ixeris polycephala* Cass. and *Pterocypsela indica* (L.) Shih.

***Paratypes*:** 2♀ and 1♂ (IMJAU), same data as holotype.

Diagnosis. The new species is easily distinguished from the other known members of the genus by the following combination of characters: head and mesosoma dark metallic green; back of gaster brown with a large yellowish patch near base, ventral

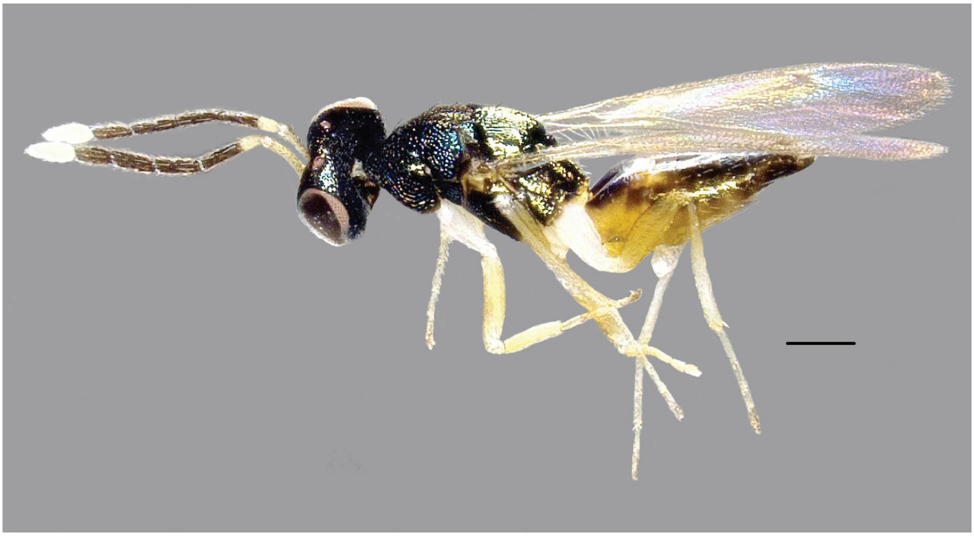


Figure 1. *Hemiptarsenus jilinus* sp. nov., female, holotype, lateral habitus. Scale bar: 200 µm.

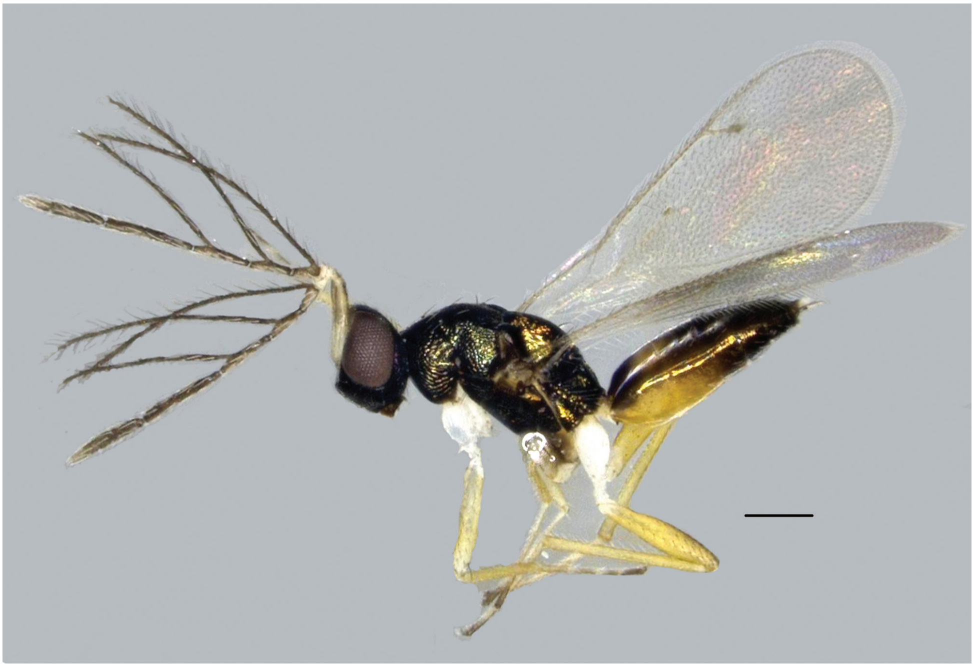


Figure 2. *Hemiptarsenus jilinus* sp. nov., male, paratype, lateral habitus. Scale bar: 200 µm.

panel of gaster yellow, apex brown; antennae (Fig. 3) with funicle dark brown, scape and pedicel pale yellow, clava uniformly white and 2-segmented; legs yellow with coxae and trochanters white; scutellum longitudinally sculptured, longer than mesoscutum;

dorsellum raised-reticulate; propodeum shorter than scutellum, with median carina and plicae complete (Fig. 7).

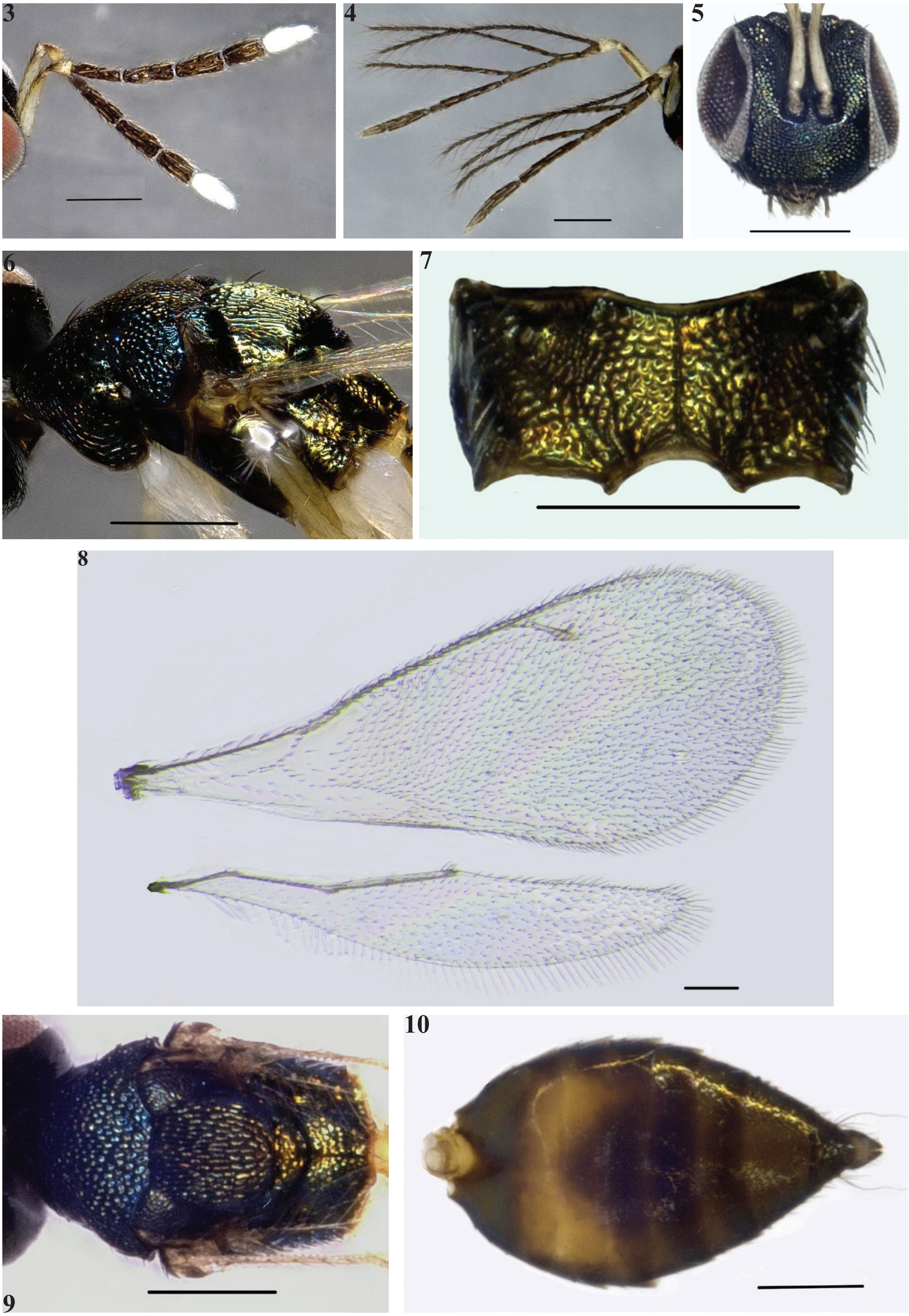
Description. Female, holotype (Fig. 1). Body length 1.68 mm, fore wing length 1.48 mm. Head and mesosoma dark metallic green. Ocelli and eyes red-brown. Antenna (Fig. 3) with funicle dark brown, scape and pedicel pale yellow. Funicle, scape and pedicel with brown setae; clava, including setae, white. Back of gaster brown with a dumbbell-shaped large yellowish patch near base, ventral panel of gaster yellow, apex brown. Legs yellowish with coxae and trochanters white. Wings hyaline with veins yellowish-brown. Callus with long, white setae.

Head in dorsal view 2.5× as wide as long, micro-reticulate, with sparse short and brown setae. POL 1.6× OOL. Head in frontal view nearly quadrate (Fig. 5), 1.1× as wide as high. Eyes bare and oval, 1.4× as long as wide. Malar space 0.4× length of eye, malar sulcus straight and obvious. Lower margin of torulus located distinctly above lower margin of eye. Distance between toruli 0.3× diameter of torulus, 0.2× distance from torulus to eye margin. Antenna (Fig. 3) with scape slender and cylindrical, 8.2× as long as wide, extending far beyond vertex; pedicel 1.8× as long as wide and scape 6.3× as long as pedicel; funicle 4-segmented, F1 2.9× as long as pedicel. Ratio of lengths of F1–4 = 1.1:1.3:1.2:1.0, segments subequal in width. Funicle with numerous longitudinal sensilla. Clava 2-segmented, basal segment 1.6× as long as distal one.

Mesosoma (Figs 6, 9) with coarse and raised reticulation dorsally and laterally, 1.6× as long as wide. Pronotum with 1 pair of black bristles. Mesoscutum (Fig. 6) slightly convex, mid lobe of mesoscutum with 2 pairs of black bristles. Notaulus inconspicuous. Scutellum longitudinally sculptured, longer than mesoscutum, with 2 pairs of stout, black bristles. Axilla micro-reticulate. Dorsellum narrow and reticulate. Propodeum (Fig. 7) shorter than scutellum, with median carina and plicae complete, propodeal spiracle small and round, callus densely setose. Middle area of propodeum between two plicae slightly elevated. Lateral and ventral panel of pronotum and prepectus with coarse reticulate sculpture. Fore wing (Fig. 8) 2.6× as long as wide. Costal cell 13.3× as long as wide, with a row of brown setae. Speculum present, but small. SMV with 6 setae on dorsal surface. Relative lengths of veins SMV:MV:PMV:STV = 15:19:9:5. Several admarginal setae present below MV. Speculum closed and basal setal line present. Precoxae with several long, white setae. Apices of pre- and mesofemora with a black spur. Femora, tibiae and tarsi of all legs with a few rows of short brown setae. Apices of tibiae of all legs with a tibial spur. Metacoxae with several short, black setae.

Metasoma (Fig. 10). Elongate-ovate in dorsal view, 1.8× as long as wide and about as long as head plus mesosoma, apex of gaster acute. Petiole short, transverse, barely visible in dorsal view. Tergites smooth, with sparse short, pale setae. Ratio of lengths of tergites = 7.0:2.5:3.0:3.5:4.0:2.0. Cercal plate with two dark setae of subequal length. Third valvula slightly exerted at apex of gaster.

Male (Fig. 2). Sexual dimorphism evident and smaller than female. Body length 1.61 mm, fore wing length 1.45 mm. Antennae (Fig. 4) with flagellum dark brown, funicle with 3 long branches, with long setae. F1 1.3× as long as pedicel. Ratio of lengths of F1–4 = 1.0:1.6:2.2:3.6. Last tarsomeres brown. Back of metasoma with a



Figures 3–10. *Hemiptarsenus jilinus* sp. nov., female (**3, 5–10**) male (**4**) **3** antenna **4** antenna **5** head, anterior view **6** mesosoma, lateral view **7** propodeum, dorsal view **8** wings **9** mesosoma, dorsal view **10** metasoma, dorsal view. Scale bars: 200 µm (**3–10**).

semicircular yellowish patch near base. Apex of metasoma obtuse. Genitalia protruding in dorsal view.

Variation. Apart from the different body sizes of specimens, the main variation is in the color. Back of scape and pedicel pale brown to yellowish; scutellum green with green metallic tinge to blue-green with purple metallic tinge; back of hind femora pale brown to yellowish.

Biology. The new species was reared from *Chromatomyia horticola* on rolled leaves of *Ixeris polycephala* and *Pterocypsela indica* Shih in Jingyuetan National Forest Park, Changchun City, where the vegetation is coniferous and broad-leaved mixed forest. The sampling site is slightly disturbed by occasional tourism.

Distribution. China (Jilin).

Etymology. The specific name is derived from the type locality's province name, Jilin Province.

Remarks. The new species is similar to *H. aditus* Narendran, 2011 in the general appearance, but differs from the latter in having: 1) Pedicel of antennae pale yellow (black in *H. aditus*); 2) Clava 2-segmented (1-segmented in *H. aditus*); 3) Dorsellum raised-reticulate (mostly smooth and shiny in *H. aditus*). 4) Propodeum with complete median carina (median carina absent in *H. aditus*) (Narendran 2011).

Discussion

In China, there are seven known members of *Hemiptarsenus*, with hosts and distributions as follows: *H. varicornis* Girault, 1913, *H. unguicellus* Zetterstedt, 1838, *H. ornatus* Nees, 1834, *H. zilahisebessi* Erdös, 1951 and *H. fulvicollis* Westwood, 1833 parasitize various species and are widely distributed (Sheng 1989; Wen et al. 2000; Zhu et al. 2000; Xu et al. 2001; Yao 2005; Pan 2019); *H. tabulaeformisi* Yang *in* Yang et al. 2015 parasitizes *Dendrolimus tabulaeformis* Tsai & Liu (Lepidoptera: Lasiocampidae) and is distributed in Beijing City (Yang et al. 2015); *H. strigiscuta* Zhu et al. 2000 is distributed in Hunan and its hosts are unknown (Zhu et al. 2000).

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RESEARCH ARTICLE

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New species and material of Hagloidea (Insecta, Ensifera) from the Yanliao biota of China

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Abstract

A new species of Cyrtophyllitinae, *Archaboilus polyneurus* **sp. nov.** Gu, Yue & Ren, is described from the Middle Jurassic Jiulongshan Formation, Daohugou Village, Inner Mongolia, China. The species is characterized by its ScA reaching the anterior wing margin at the level of the divergence of M+ CuA, distally branched RP, lengths of free CuA and free M equal, and numerous branches of CuA + CuPaα. A new fossil of *Liassophyllum caii* Gu & Ren, 2012 is described which increases knowledge of its wing venation and indicates that *Liassophyllum* should be assigned to the Tuphellidae.

Keywords

Archaboilus, Daohugou, Cyrtophyllitinae, *Liassophyllum*, Middle Jurassic, Orthoptera, systematic palaeontology, Tuphellidae

Introduction

The superfamily Hagloidea (Orthoptera) sensu Gorochov 1995 was widespread from the Late Triassic to the Early Cretaceous and consists of the families Haglidae, Tuphellidae, Prophalangopsidae, Hagloedischiidae (Gorochov 1995). A cladistic analysis based on wing venation suggests that it is paraphyletic (Béthoux and Nel 2002).

The Prezottophlebiidae was erected by Martins-Neto (2007) and assigned to the Hagloidea on the basis of a new species from the Early Cretaceous Santana Formation of Brazil. Although Haglidae are extinct and Prophalangopsidae are now considered to be relicts, they are the most diverse Hagloidea in the fossil record (Gorochov 1995; Wappler 2001; Gu et al. 2010).

The non-marine Jurassic and Cretaceous deposits of northern China are rich and diverse in fossil insects (Wang et al. 2012; Cai and Huang 2014; Fang et al. 2020; Gao et al. 2021; Yang et al. 2021). In the Yanliao and Jehol biota, Prophalangopsidae are the most diverse and abundant Orthoptera with over thirty valid species, while the Haglidae have lower diversity and abundance. Lin (1965) described two haglid species from the Lower Jurassic of Inner Mongolia, but they were erected based on female wings, which are difficult to compare with known haglid species, which are based on males. *Alloma* Hong, 1982 (Hong 1982a) and *Hebeihagla* Hong, 1982 (Hong 1982b), are considered as synonyms of *Parahagla* Sharov, 1968 of Chifengiinae, which were originally assigned to Haglinae of Haglidae (Hong 1982a, b). The family assignment of *Yenshania hebeiensis* Hong, 1982 (Hong 1982a) is questionable, as the type specimen is very fragmentary. Although *Isfaroptera yujiagouensis* Hong, 1983 was also erected based on a very fragmentary specimen, its preserved characters are sufficient to support its assignment to Haglidae. Gu et al. (2012a, b) described two Jurassic hagloid species, *Archaboilus musicus* Gu, Engel & Ren, 2012, and *Liassophyllum caii* Gu & Ren, 2012. The broad winged species *Vitimoilus* ovatus Gu, Tian, Yin, Shi & Ren, 2017, was described from the Early Cretaceous Dabeigou Formation, the most recently described haglid species from China (Gu et al. 2017).

Here, we report a new species of the haglid subfamily Cyrtophyllitinae and describe a new fossil of *Liassophyllum caii* Gu & Ren, 2012, increasing the diversity of Haglidae and knowledge of their wing venation.

Method and materials

The specimens were examined with a Nikon SMZ 25 microscope and photographed with a Nikon DS-Ri 2 digital camera system. Line drawings were prepared using Adobe Illustrator CC 2017 and Adobe Photoshop CC 2017 software. Measurements were taken using Adobe Illustrator. The specimens are housed at the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University (CNU), Beijing, China.

Wing venation terminology follows the interpretation proposed by Béthoux and Nel (2002). Another commonly used Orthoptera venational terminology is that of Sharov (1968; and see e.g., Gorochov 1995). These mainly differ by their interpretations of the media and cubitus areas. For ease of comparison, we also provide the Sharov venation system in parentheses. Corresponding abbreviations used are: ScA (C), anterior subcosta; ScP (Sc), posterior subcosta; RA (RA), RP (Rs), anterior and posterior radius, respectively; MA (MA1), MP (MA2), anterior, posterior media, respectively; CuA (MP), CuP, anterior, posterior cubitus, respectively; CuPaα (CuA1), the anterior branch of first posterior cubitus; CuPaβ (CuA2), the posterior branch of first posterior cubitus; CuPb (CuP), the second posterior cubitus; AA1 (1A), first branch of anterior anal vein.

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Orthoptera Olivier, 1789
Suborder Ensifera Chopard, 1920
Superfamily Hagloidea Handlirsch, 1906
Family Haglidae Handlirsch, 1906
Subfamily Cyrtophyllitinae Zeuner, 1937

Archaboilus **Martynov, 1937**

Composition. *A. kisylkiensis* Martynov, 1937, *A.martynovi* Gorochov, 1988, *A. musicus* Gu, Engel & Ren, 2012, *A. shurabicus* Martynov, 1937, *A.similis* Zherikhin, 1985, *Archaboilus polyneurus* sp. nov.

Archaboilus polyneurus **sp. nov. Gu, Yue & Ren**

http://zoobank.org/59886EC8-2ABE-4064-868D-8A0867FE5F34
Fig. 1

Diagnosis. ScA reaches anterior wing margin at level of divergence of M+ CuA, RP branched distally, lengths of free CuA and free M equal, CuA + CuPaα with numerous branches.

Material examined. ***Holotype***, CNU-ORT-NN2009018PC. ***Paratype***, CNU-ORT-NN2009011.

Locality and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Bathonian–Callovian boundary interval (Ren et al. 2019), Middle Jurassic.

Description. Forewing oval, estimated length ca 33 mm. ScA crossing area between ScP and anterior wing margin, reaching margin at level of divergence of M+ CuA; basal part of ScP slightly anteriorly curved, ScP reaching anterior margin at 3/4 to wing base with numerous oblique branches uniformly distributed; branches of ScP with secondary vein between them, formed by two rows of cells; most cross-veins between ScP and R straight; stem R slightly undulate; RA basally branched, pectinate with 4–7 terminal branches; base of RP curved towards to posterior margin, RP very distally branched with less branches than RA; area between RA and RP with series of regular arranged cross-veins; area between R and M expanding when R dichotomous, with series of long cross-veins, cross-veins of expanded area curved; presence

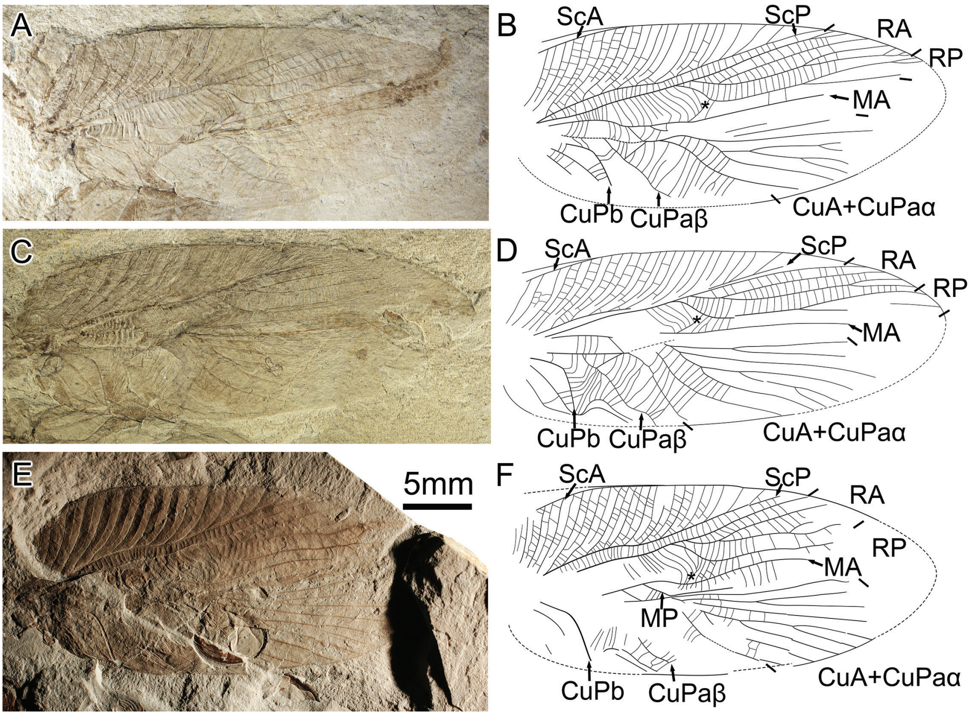

Figure 1. Photos and drawings of *Archaboilus polyneurus* sp. nov. Gu, Yue & Ren, asterisk indicates the transverse veinlet connecting MA and base of RP. **A–D** right and left forewing of the holotype, CNU-ORT-NN2009018C **E, F** CNU-ORT-NN2009011. Scale bar: 5 mm.

of a transverse veinlet connecting MA and base of RP (asterisk on Fig. 1B, D, F); M separated from M + CuA distant to origin of RP; MA probably undulate; MP strongly curved basally (not preserved in holotype); lengths of free CuA and free M equal; CuA + CuPaα with numerous branches; CuPaβ oblique; "handle" straight; CuPb strongly oblique, basal part and middle part (where bearing teeth) forms obtuse angle.

Etymology. From the Latin "*polyneurus*", referring to its numerous branches of CuA + CuPaα.

Discussion. Although the preservation and deformation of the specimens makes it difficult to identify the complete structure of ScA, this new species can be assigned to *Archaboilus* Martynov, 1937 by a combination of its ScA crossing the area between ScP and the anterior wing margin, the base of MP strongly curved, and the presence of a transverse veinlet connecting MA and the base of RP. Besides these diagnostic characters of the genus, *A. polyneurus* sp. nov. shares with *A. musicus* from the same locality a slightly sigmoidal ScP, but it differs from it by its much more distally branched RP and distinctly smaller forewing. Although the holotype and single known specimen of *A. kisylkiensis* Martynov, 1937 is only the basal half of a forewing, its free CuA is much longer than its free M, not as in the new species. *A. polyneurus* sp. nov. differs from all other *Archaboilus* species by its shorter ScA, very distally branches of RP, and numerous branches of CuA + CuPaα. Although the terminals numbers of RA and CuA + CuPaα are different between the holotype and paratype, this kind of difference has been shown to be intra-specific variation in orthopterans and their relatives (Béthoux 2008; Gu et al. 2010, 2011).

Family Tuphellidae Gorochov, 1988
Genus *Liassophyllum* Zeuner, 1935

Liassophyllum caii Gu & Ren, 2012
Fig. 2

Material examined. CNU-ORT-NN2020001.

Locality and age. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Bathonian–Callovian boundary interval (Ren et al. 2019), Middle Jurassic.

Description of new material. Isolated left forewing with negative and positive imprint; preserved length 41 mm, estimated complete length ca 49 mm, distal part of subcostal area, R, M, part of posterior margin all missing. Preserved forewing venation

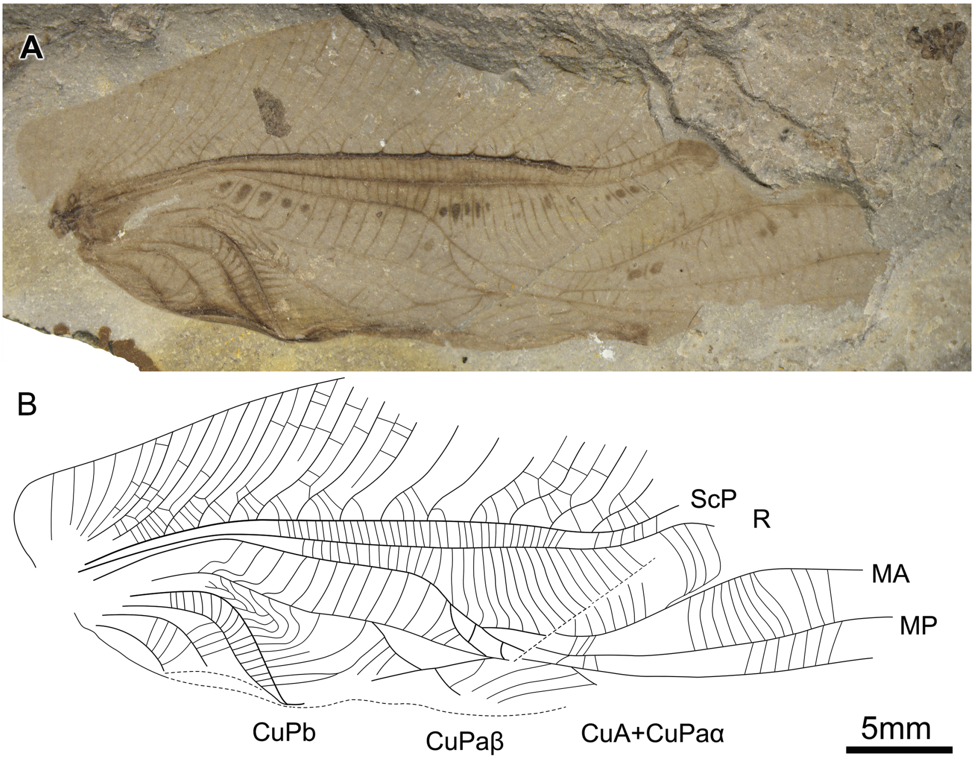

Figure 2. Photo (**A**) and drawing (**B**) of *Liassophyllum caii* Gu & Ren, 2012, CNU-ORT-NN2020001. Scale bar: 5 mm.

almost the same as previously described fossils of the species. Forewing elongated, not typically oval; the anterior wing margin is slightly flattened in its basal part, then arched upwards; there is no curved ScA crossing area between ScP and anterior wing margin; area between ScP and anterior margin basally narrowed, gradually widened to the middle; area between CuPb and CuPaβ broad, very basal cross-veins strongly curved and connected, formed into several irregular cells.

Discussion. Although the distal part of the forewing is absent, we assign the new fossil to *L. caii* Gu & Ren, 2012 by the following: R is simple for a long distance and is strongly arched toward the anterior margin distal to the redirection of ScP; MA is undulate; and the area between R and MA is distinctly broad. *Liassophyllum caii* Gu & Ren, 2012 was erected based on 11 specimens. The holotype is an isolate forewing with the basal area between ScP and the anterior margin missing, the paratypes are well preserved but with wings strongly overlapped and their subcostal area is not clear. The basal part of the subcostal area of the type species *L. abbreviatum* Zeuner, 1935 is also unknown. The new material described here has a clear subcostal area, improving the knowledge of this important area. It lacks an arched ScA crossing the subcostal area positioned very close to the anterior wing margin. The basal-most area between ScP and anterior wing margin has fan-like veinlets. Zeuner (1939) and Gu et al. (2012a) attributed *Liassophyllum* to Cyrtophyllitinae, but Gorochov (1995) and Gorochov et al. (2006) excluded the genus from the subfamily, not mentioning its higher-rank assignment. The new material reported here supports exclusion of *Liassophyllum* from the Cyrtophyllitinae by its absence of an arched ScA crossing the area between ScP and the anterior margin. Further, the undulate MA, the long and more or less undulate stem of R, the very distal dichotomous R, and the broad and long area between CuPb and CuPaβ of *Liassophyllum* species strongly indicate that this genus belongs to the Tuphellidae.

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COMMENTARY

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Response to Zamani et al. (2020): The omission of critical data in the pursuit of "revolutionary" methods to accelerate the description of species

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Abstract

Here we respond to the criticisms leveled against a proposal that suggested an efficient solution to the taxonomic impediment. We clarify some of our objectives and demonstrate that many of the criticisms apply more to traditional approaches to taxonomy rather than to our minimalist approach.

Introduction

Zamani et al. (2020) criticized a solution to the taxonomic impediment proposed in Meierotto et al. (2019), who employed COI barcodes plus a single photograph as diagnostics. The authors of this rebuttal are in full agreement that a diagnostic method similar to the Meierotto et al. and the follow-up Sharkey et al. (2021) approach is needed in groups with overwhelming diversity and little likelihood of ever being treated in a morphological revision. Examples of such groups are the phorid fly genus *Megaselia* Rondani, which is estimated to have close to 1000 species in northeastern Costa Rica alone, and many genera of Neotropical Braconidae, some of which were the subjects of the Meierotto et al. and Sharkey et al. papers. Although the Zamani et al. critique touched on many subjects with which we disagree, we limit our response to what we see as key issues that were not comprehensively addressed in Sharkey et al. (2021).

Much of what Zamani et al. demanded as ***required*** taxonomic procedure is opinion. Taxonomy can proceed in different ways, with different phases of completeness. Detailed treatment of all life stages of an insect, for instance, frequently postdates the description of that species, which is often based on a single sex. Aspects of variation, distribution, life history, etc. are often included later, long after the species is described. Meierotto et al. (2019) took this concept one step further. Using DNA barcoding, which usually allows for a more precise recognition of species, they proposed to defer almost all aspects of species description other than a diagnosis based on COI gene sequence and a photograph. Future revisers may include these omitted details by examining specimens in greater depth, should there be the desire and finances to do so.

The first and perhaps most emphasized criticism of their article was that the, "authors failed to diagnose their 15 new *Zelomorpha* Ashmead, 1900 species from 51 out of 52 previously known species". An important note is that the molecular diagnoses employed are recognized as valid diagnoses according to the code of zoological nomenclature. In Meierotto et al. it was emphasized that the second author had seen all of the types and that none but *Z. arizonensis* were, in his opinion, conspecific with described species; however, let's imagine that this was not true and that Meierotto et al. ignored most of the previously described species; i.e., those lacking COI barcode sequences, essentially all but one. The COI barcode is very effective in diagnosing species of *Zelomorpha* and if a previously described species of *Zelomorpha* was barcoded and found to be very (very) similar or identical to one that Meierotto et al. described, their new species hypotheses would be falsified (or reasonably so). That is an effective diagnostic. The type specimens need not be barcoded. Just as in the case of *Zelomorpha arizonensis*, a specimen fitting the description and locality of the type could be barcoded as a proxy. In many groups of organisms in which the majority of the species are described this would not be a viable alternative, however in hyper-diverse groups with only a small percentage of the fauna described the problems created are few and they are far outweighed by the advantages.

Here are the reasons for temporarily ignoring the previously described species and producing barcode-only diagnoses. 1. It allows for the efficient and quick diagnosis of species. 2. No one uses morphological keys and diagnoses to these hyper-diverse taxa, because they do not work. 3. The only way to even suspect that a newly discovered specimen belongs to a morphologically described species is to borrow all related types and visit museums, mostly scattered across Europe and North America. 4. There are so many species in these groups that a morphological key to the small percentage of described forms has little value.

The first reason is explained elsewhere in this article and in Sharkey et al. (2021) so we begin with the second reason, i.e., no one uses the keys and diagnoses in these hyper-diverse groups. There are very few revisionary studies on species-rich genera of braconids in the tropics, but here we will look at statistics for the revision of *Alabagrus* Enderlein, 1920 by Sharkey (1988).

The revision of *Alabagrus* included 104 species treated with morphology only. It contained a key as well as diagnoses and descriptions of each species and was heavily critiqued by Sharkey et al. (2021). According to a search in Google Scholar, the *Alabagrus* revision has 32 citations. The majority of the citations are surveys that simply copy the distributional records that are in the paper. For example, Coronado-Blanco et al. (2016) surveyed the literature for all Agathidinae occurring in Mexico and included the number of species cited as being present in Mexico by Sharkey (1988); the keys and descriptions were not employed.

There are about four citations for the *Alabagrus* revision in which the publication was used to identify a specimen, but in only one of these was the identification verified by anyone other than Sharkey. In this sole citation, a parasitoid of a new Nearctic species of Crambidae, *Diatraea mitteri*, was identified by as *Alabagrus imitatus* (Solis et al. 2015). The key has not been used for any of the Neotropical species where 98% of the diversity lies.

It took Sharkey over seven years and a prolonged trip to Europe to view types to produce the revision and it is worse than useless, because it is full of misleading information on species limits and species distributions. Some might argue for an integrative approach, such as the revision of Costa Rican *Alabagrus* by Sharkey et al. (2018), but what is the point of including morphological descriptions and keys when the COI barcode is the only reliable source for identification? There appears to be good reason to ban revisions based solely on morphology rather than those based primarily on COI barcodes.

The third reason, to temporarily ignore old type specimens until they, or proxies, are barcoded, is the expense and difficulty of viewing them. The only way to even suspect that a newly discovered specimen belongs to a described species is to borrow all relevant types and probably visit museums mostly scattered across Europe and North America. The first problem that a reviser would come across for a revision of *Zelomorpha* would be to find the types of the 52 species of *Zelomorpha* that had been described. Since Sharkey has already done this we can report that it is not possible to find these in the literature. Species of *Zelomorpha* have been described under at least 13 different generic names, i.e., *Agathis*, *Biroia*, *Bracon*, *Chromomicrodus*, *Coccygidium*, *Crassomicrodus*, *Cremnops*, *Dichelosus*, *Disophrys*, *Ichneumon*, *Microdus*, *Spilomicrodus*, and *Zelomorpha*. Most of these are species described by taxonomists in the late 19th and early 20th centuries, therefore the descriptions are brief and all but useless. A reviser would have to visit 12 different museums in 10 different countries [Poland, Hungary, France, Germany, USA (Washington D.C.), USA (Philadelphia), USA (New York), England, Sweden, Costa Rica, Denmark, and Italy] and look at all of their agathidines to "rediscover" the 52 species. After looking at these species there would be many that certainly are not among the species being revised and these could be maintained. The problem occurs when a museum specimen is a close match with a specimen in hand. If not identical and from the same locality as the holotype, morphological similarity is not enough to indicate conspecificity. The article by Sharkey et al. (2021) clearly documents this, as does the revision by Sharkey et al. (2018) in which even with barcodes some species could not be differentiated morphologically. Another example, and there are thousands, is in the phorid genus *Megaselia*, in which 16 species were masquerading as one in collections, until molecular data were collected (Brown et al. in review). In hindsight, a few of these can be identified using morphological characters, but most cannot, even though they have deep COI divergences.

Morphological diagnoses necessitate the viewing of holotypes and as such they act as an enormous impediment to the taxonomy of hyper-diverse taxa. There are also social and environmental issues to consider. The cost of travelling to the museums to view types is expensive, all but precluding the participation of taxonomists from developing countries. There is a cost to the environment in the air travel involved, and finally in the case of pandemics, such as the one currently being experienced (Covid-19), virtually no one can visit museums. Consider the alternative when the barcode serves as a proxy to the holotype; a simple search on BOLD (Barcode of Life Datasystem) will indicate with a great degree of certainty whether a specimen belongs to a described species.

The final argument, for postponing the inclusion of non-barcoded species in our species-rich genera, is the low probability that newly discovered specimens have been described. We estimate that there are approximately 500 species of *Zelomorpha*. With only 52 described there is only a 10% chance that a newly described species will be a synonym. Compare this to the current 33% synonymy rate for species of Ichneumonoidea as documented by Yu et al. (2016). We can also imagine a day in which all 500 species of *Zelomorpha* are described and there is a morphological key to them all. Such a key, if dichotomous, would be about 700 couplets long. Anyone familiar with long keys will know that the longer the key is, the higher the probability of error is. Multiple entry keys such as Delta and Lucid can reduce the decisions required for identification but the probability of success would still be minimal. In summary we feel that little is lost if types are ignored until they or their proxies are barcoded, and we emphasize that barcoding types should be a priority for museums. We further suggest that it is time to stop describing members of these species-rich genera based on morphology alone.

Zamani et al.'s statements that more than one photograph should be required and that text elucidating important diagnostic characters should be included are irrelevant because ***we don't expect anyone to identify these species using morphology***. For some groups of insects (we are not saying for all groups), the idea that people, even experts, can accurately identify species using morphology is wrong, as documented separately (Sharkey et al. 2021; Brown et al., in review). For instance, hand a *Megaselia* specimen from Costa Rica to a phorid taxonomist, and outside of a couple of well-known species, the possibility of getting an identification back is almost zero. Experts can try to run the specimen through the inadequate keys (that treat only a small fraction of the 2000+ species estimated from Costa Rica), compare it to the broken, shriveled types, and perhaps look through the almost non-existent identified collections to try to get close. But even if a specimen is matched to a description, that specimen might be one of a group of cryptic species that may not be recognizable (using some extremely minute or subtle morphological character) without sequence data. With a likely total of over 2,000 species of Costa Rican *Megaselia*, this situation will not change soon, if ever.

Users of biodiversity information need to be able to recognize species. This will never occur using morphology alone in most species-rich groups of insects with cryptic morphologies. Such organisms require huge amounts of time to diagnose, with required dissections, drawings, and incorporation into ever-longer keys with more and more complicated exceptions. Additionally, such morphological keys need to be generated for all life stages separately, seriously compromising a system based solely on morphology. DNA barcodes have a huge benefit of permitting species delimitation and specimen identification regardless of life history stage, and usually also sample condition.

To us, one of the least-appealing aspects of the realization that barcoding is necessary is the loss of the fantasy that we can sit down with a specimen at a microscope and definitively arrive at a species name for it. This type of immediate identification in some highly diverse groups of insects is a taxonomic fiction. Until we have individual-sized barcoders, which are not far off (Pomerantz et al. 2018), identification in groups, such as Neotropical Braconidae and Phoridae, is an event involving the processing of at least one 96-well plate of specimens. Taxonomists can come close (such as a genus, or species-group identification), but nobody should need to spend 10–30 minutes in a usually futile attempt to identify a specimen when anyone can obtain a conclusive answer with barcodes, 96 at a time. A taxonomist's time is too valuable for this; instead, they should be overseeing the results of barcoding, looking for errors, split or lumped taxa that occur at extremely low levels in barcoding (much lower levels than with morphological taxonomy, in our experience), not to mention publishing the new species that have been discriminated by COI sequences. Costs for this procedure will decrease dramatically over time, and we have to prepare for this reality now. In fact, some of the newest high-throughput platforms, notably those by Pacific Biosciences, already allow analyses of thousands (SEQUEL I) (Hebert et al. 2018) or tens of thousands (with the newest upgrade of SEQUEL II) of specimens at costs ($1–$2 USD) that are only a fragment of those of the Sanger methods. This unprecedented progress on the DNA sequencing technology front seriously challenges the cost-efficiency of morphology-based description and identification approaches under most circumstances.

One oft-repeated criticism of this approach (in both Zamani et al., and in a barrage of social media posts) is that it discriminates against entomologists in developing countries, where funding for this type of work might not exist. This argument is beside the point for groups like ours that have so many species that morphology simply does not work. It is not DNA taxonomy that is the problem for scientists in developing countries; it is the large groups that cannot be treated in the traditional way. If critics want to argue that it is better to leave these groups "undone" than to treat them in a way that some cannot afford to replicate, we have to respectfully disagree.

Zamani et al.'s comments invite contemplation about the target audience for longer descriptions. Applied users of biodiversity information (conservation biologists, ecologists) don't need to know how many notopleural setae a fly has; however, they need to identify specimens, know which species are present in a given area, and where else a given species might occur. The exhaustive descriptions of most taxonomists of hyperdiverse groups only serve themselves and a few other taxonomists; in fact, we venture a bet that few have used the species-level keys in major taxonomic revisions of hyper-diverse genera of Ichneumonoidea, Phoridae and many others. Despite the fact that there are tens of thousands of species in these groups, there are very few major revisions.

Meanwhile, as we generate time-consuming morphological treatments of a very small percentage of our faunas, global warming is on the rise, wildfires are burning at record rates, the loss of natural habitats is accelerating, and thousands of species are going extinct. It is important to note that the small fraction of all species so far described largely represent the less diverse groups with large body size, and that this work has mostly been done in the least biodiverse areas such as Europe. It is, therefore, foreseeable that taxonomic work, if continuing to rely largely on morphology, will progress even more slowly and become increasingly complex than during the past ~260 years. We do not have time to wait but must find novel and better solutions for the taxonomic crisis.

Stating that our form of description, as a first-pass step for taxonomy, is unacceptable, sloppy, or lazy is untrue; it is simply efficient towards a different goal. A DNA-based taxonomy will quickly make species known in large numbers that otherwise would remain in obscurity. The critics' concern about description quality seems to be conflating comprehensiveness of descriptions (how many characters are mentioned or illustrated) with accuracy of the descriptions. We are concerned with accurately and concisely describing new species. Therefore, possible objections to DNA-based species are that they aren't real species and that the species we describe cannot be recognized later by other researchers.

The reality of species could be argued ad nauseam depending on one's preferred species concept. As speciation is a process rather than an event, delimitation of species is also inherently subjective, for example with allopatric populations slowly diverging apart (Mutanen et al. 2012). We argue that DNA-based species as identified by BINs in BOLD are highly objective and congruent with species identified using multiple genes more than 90% of the time for our taxa, phorid flies and braconid wasps. For the latter, the success rate is 98% (Sharkey et al. 2021). This experience is at odds with Meier and Zhang (2009), who cite a 34% error rate in a data set from another public database, GenBank, but we suspect that their number is a product of "operational" errors, such as incorrect identifications in GenBank, contaminated sequences, incomplete sequences, and other easily-corrected items that would be amended in any serious taxonomic analysis. Furthermore, such comparisons typically assume the reference taxonomy, usually morphology-based, to be accurate, which hardly ever is true (Mutanen et al. 2016). We find a much lower discrepancy in BOLD, with only a few BINs needing refinement by taxonomists, either by examining the morphology of specimens, ecological factors like host use, or patterns of COI divergence. This experience tells us that intelligent shortcuts are possible in completing the inventory of large groups. Admittedly, study of interesting information about the structure and evolution of these species is deferred until later, but this is in service of the priorities of those needing biodiversity data now (ecologists and conservation biologists), rather than the systematists who want a better understanding of their group.

Another criticism is the poor quality of images. We agree with this concern, which was a mechanical problem in the processing of the article, which has now been resolved for both the Meierotto et al. and Sharkey et al. (2021) publications.

We share the same ideals as Zamani et al. concerning taxonomic treatments, i.e., employing multiple genes to elucidate species boundaries and place species in a phylogenetic context, multiple images of each holotype and other specimens to show variation, an illustrated morphological key, and a concise morphological diagnosis, e.g., Sharkey et al. (2018), Brown (2006), Brown and LeBrun (2010). As clearly documented by Meierotto et al., given the number of undescribed species of Ichneumonoidea and the current rate of species descriptions, it would take thousands of years to treat all Ichneumonoidea with this level of detail. We suggest that the Meierotto et al. approach, or something akin to it, is the most promising proposed solution that can act as a first taxonomic pass and one that can easily be built upon when time, money, and desire permit. Currently, the most productive 10 ichneumonologists each describe approximately 500 species in a lifetime. With the Meierotto et al. approach it will be easy for a productive taxonomist to treat 1000 species each year. For example, in our first attempt at a large species treatment, Sharkey et al. (2021) described more than 400 new species of Costa Rican braconids while trying to streamline the process. Fifty years from now we could have 20,000 ichneumonoid species treated the conservative way or one million using the Meierotto et al. approach (20 taxonomists × 1000 species per year × 50 years). One million species is the current estimate we have for total ichneumonoid species-richness. These two approaches are not mutually exclusive, and the species recognized using the Meierotto et al. approach may drastically increase the rate of more thorough second pass revisions.

A point made by Zamani et al. is that mitochondrial diagnoses are flawed because "*Wolbachia* may be altering mtDNA introgression" and "mitochondrial trees often disagree with nuclear species trees." This has been shown to be true in some cases (Klopfstein et al. 2016, Ivanov et al. 2018); however, as a first pass, DNA barcoding will still outperform morphology-based species recognition for highly cryptic taxa. Additional splitting of species that are discovered to share COI sequences may be necessary if more genetic data are acquired, but this is no different than any other taxonomic revisionary approach.

Zamani et al. opined that DNA-based descriptions will make the identification of millions of historical specimens impossible. This is only a short-term problem, however, as technology is rapidly improving the sequence capture rate of historical specimens. Once this technological hurdle is passed, collections will be gold mines of information on the historical distributions of species (many of which will presumably be extinct). "Museomics" is indeed a rapidly developing area of taxonomy, including DNA barcoding (Prosser et al. 2016); for example, the Finnish Barcode of Life initiative is presently barcoding old museum specimens, including types, on a large-scale.

Zamani et al. were inaccurate in their statement, "Simply assigning all BINs taxonomic names as Meierotto et al. (2019) propose would indeed complete the inventory of life on Earth extremely quickly". This is a potential solution; however, Meierotto et al. did not advocate this approach for several reasons. The most relevant is that BINs do not equal species: more than one species may occupy a BIN, and even more rarely a species may occupy more than one BIN. A 2% genetic distance is the conventional threshold for species delimitation using COI barcodes (Jones et al. 2011), and this is used to cluster putative species, but it is not infallible and was never proposed as such

(Ratnasingham and Hebert 2013). For example, in their treatment of Costa Rican braconids, Sharkey et al. (2021) found seven species of *Macrocentrus* in one BIN, and this necessitated a morphological key to differentiate them (although their COI sequences also distinguished them but not at a level to allow for separate BIN placements). Another potential problem is contamination in cases where a COI barcode is assigned to the wrong specimen. This also requires an examination of the specimens and some expertise. Finally, it takes a great deal of expertise to identify any specimen in our diverse taxa to the generic level, and this is a necessary first step for any revision. Zamani et al. complained that the approach would supplant taxonomists with technicians. This is neither entirely true nor entirely problematic. Technicians will play an increasingly important role, and many of the co-authors of the Sharkey et al. (2021) treatment of Costa Rican braconids fit the technician category. Enabling technicians to do much of the data acquisition will reciprocally enable taxonomists to focus their time and effort on problems that require their expertise.

Zamani et al. suggest that, "a true paradigm shift in taxonomy will come only when there is a revolution in the level of financial investment in taxonomy". We have heard this for decades as resources for alpha taxonomy steadily decline. This cry for help is ignored by the general public and by scientists in other disciplines. Many taxonomists fail to realize that 99.99 percent of the public have no idea what we do and could not care less about the description of a new species of *Zelomorpha* or any other insect. Greatly increased funding for alpha taxonomy will never happen unless we taxonomists can demonstrate to funding agencies that we can overcome the taxonomic impediment in a reasonable timeframe with a reasonable budget. This could be done if those of us working on understudied, hyper-diverse taxa employed an approach similar to the one outlined by Meierotto et al. (2019) and Sharkey et al. (2021). Science funders seem to agree with this statement and three examples follow. The International Barcode of Life (iBOL) and its participatory nations raised $125 million for the first phase of BARCODE 500K (https://ibol.org/programs/barcode-500k/). The BioAlfa project, supported by Costa Rican government and others (https://www.gdfcf.org/bioalfa-bioliteracy-costa-rica), has begun to barcode all of Costa Rica's multicellular terrestrial life-forms over ten years, with millions of dollars in start-up funding and sweat equity. And finally, the European Research Council awarded ~12 million Euros for the global-scale biodiversity initiative LIFEPLAN, with massive DNA barcoding being at its heart (https://www2.helsinki.fi/en/projects/lifeplan).

It is interesting to contemplate the degree of damage that could be done to the taxonomy of a group if the worst nightmares of Zamani et al. were realized and a DNA-based description paradigm was widely adopted. Many species would be described quickly, some incorrectly. Perhaps 1% of descriptions (based on Sharkey's observations in Braconidae; perhaps more in some other groups) would be wrong or need further fine-tuning. Compare this to the 33% synonymy rate for ichneumonoids that can be extrapolated from Taxapad (Yu et al. 2016). In the last update of this database in 2016, there were 44,385 valid species names and 13,606 synonyms. This 33% synonymy rate does not include lumped species, i.e., species concepts that contain more than one species, which is an even more prevalent source of error. Meanwhile, thousands of new species would be known that would have remained in obscurity. There would be photographs, the means to recognize them based on barcodes, and type material deposited in museums. It is an imperfect system, but it leads to progress on groups that will otherwise remain untouched for decades or perhaps forever. Who, for example, is going to describe the estimated 1,800,000 species of gall midges (Cecidomyiidae) (Hebert et al. 2016)? The answer is obvious; nobody will do it unless new, fast, efficient methods are employed.

For those readers that see the rationale in the above arguments, the question becomes how to effect this change. To implement a survey of megadiverse taxa, it is financially, and in many other respects, impractical to attempt to survey the entire world now. However, all long journeys begin with a few tentative steps, and adoption of DNA-based methods for sorting large collections of specimens is a positive development that will move us closer to this goal.

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Corrigenda: Morphological and molecular evidence support the taxonomic separation of the medically important Neotropical spiders *Phoneutria depilata* (Strand, 1909) and *P. boliviensis* (F.O. Pickard-Cambridge, 1897) (Araneae, Ctenidae). ZooKeys 1022: 13–50. https://doi.org/10.3897/zookeys.1022.60571

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In a recent publication (Hazzi and Hormiga 2021) we demonstrated that there are two species under the name of the ctenid spider *Phoneutria boliviensis* (F.O. Pickard-Cambridge, 1897) and used the name *Phoneutria depilata* (Strand, 1909) for this second species, which in the past had been treated as a junior synonym of *boliviensis*. We proposed that "*Ctenus peregrinoides* Strand, 1910" was a new junior synonym of *Phoneutria depilata*. We note here that such synonymy is an error. The problem resides in the fact that the name "*Ctenus peregrinoides*" is not available based on the Criteria of Availability of the ICZN (1999), of which Articles 10 and 11–20 must be satisfied. Article 11.5 states that: "Names to be used as valid when proposed. To be available, a name must be used as valid for a taxon when proposed, unless it was first published as a junior synonym and subsequently made available under the provisions of Article 11.6.1" (ICZN 1999).

This requirement is not satisfied by Strand's provisional name "*C. peregrinoides*." Strand (1909a: 318) described two females from Guatemala under the name *Ctenus peregrinus* F.O. Pickard-Cambridge, 1900, and noted some differences with Pickard-Cambridge's illustration of *peregrinus* in 'Biologia Centrali Americana', stating that "Sollte die Art neu sein, möge sie *peregrinoides* m. genannt warden" ("If the species is new, it may be called *peregrinoides*"). Thus, Strand did not use the name "*Ctenus peregrinoides*" as valid when he proposed it (valid as opposed to, for example, "if this were a new species, here is a name"), which means that his provisional name is not available for nomenclatural purposes. Formally treating "*peregrinoides*" as a junior synonym is inconsequential because Strand's name is not available in a nomenclatural sense.

Furthermore, we need to correct the exact publication dates of the two relevant works of Strand (1909a, b). The unavailable name "*peregrinoides*" was published on 21 October,1909. A couple of months later (21 December 1909) Strand described *Ctenus depilatus*. The fact that these two publications appeared both in the 28th issue of Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere, which corresponded to 1910 (as printed in the frontispiece of the journal), has been a source of confusion regarding the publication dates. While Roewer (1955: 649 for *C. depilatus*; 654 for *C. peregrinus*) correctly lists both of them as published in 1909, the catalogs of Petrunkevitch (1911: 413, 476) and Bonnet (1956: 1279, 1287) list them as published in 1910.

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