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Some remarkably common, but undescribed, *Megaselia* Rondani (Diptera: Phoridae) from northwestern Costa Rica

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Abstract

A collection of 16,521 barcoded phorid flies from Área de Conservación Guanacaste (ACG) in northwestern Costa Rica contains 1,498 recognized BINs (Barcode Index Numbers) in the BOLD database. These BINs were identified to genus, based on photographs, and the collection was found to be composed largely (893/1,498=60%) of specimens of the enormous genus *Megaselia* Rondani. The nine most common ACG *Megaselia*, represented by 100 or more specimens each, are briefly described, and diagnosed largely based on DNA barcodes. This study is a prelude and pilot to naming the many less-common species in a similar format.

key words: tropical, biodiversity, DNA taxonomy, insects, faunistics

Introduction

The genus *Megaselia* Rondani (Diptera: Phoridae) is one of the largest of all insect genera. Its monophyly is doubtful, however (Brown 1992; Disney 1989; Hartop *et al.* 2020), and it remains a taxonomic quagmire, with thousands of undescribed species and only a few (about 1,700) described worldwide. The lifestyles of the few species for which we have information are as scavengers, predators, parasitoids, fungivores, and herbivores (reviewed by Brown 2018; Disney 1994).

In the Neotropical Region from Mexico to Argentina, there are about 350 described species of *Megaselia*, and only 47 described or formally identified from Costa Rica. Virtually all of these species are represented in the literature simply as original descriptions and citations of the catalog of world species (Borgmeier 1968); in other words, nobody is using these names. Therefore, implementing a largely DNA-based taxonomy for *Megaselia*, using DNA barcodes and table-based descriptions (Hartop & Brown 2014, Hartop *et al.* 2015, 2016) to rapidly name species, and make them available for ecological and conservation analyses and other applied uses (e.g., Janzen & Hallwachs 2020), is desirable.

Naming of new species are usually made within the context of revisions of many other similar species, but with a group as large and poorly-known as Neotropical *Megaselia*, the chances of anyone doing a traditional generic revision is close to zero. I therefore instead propose naming of some new species of *Megaselia* encountered during an ongoing, large-scale inventory. This is a change from normal procedure: in this new system, species are named to establish (mostly) DNA barcode diagnoses, usable names, and type specimens. The result might seem highly incomplete to some systematists (e.g., Wheeler 2018; Zamani *et al.* 2020), as issues of morphological recognition are not investigated in detail, but the result is a first step towards actually completing the Costa Rican phorid inventory. Given that there are estimated to be many thousands of *Megaselia* species in Costa Rica, the reduced format makes an otherwise unattainable goal possible. More comprehensive studies of morphology can be later added when desired for additional purposes (e.g., morphological sorting and phylogenetic character analysis).

In this paper, I name a nine of the *Megaselia* from the Costa Rican ACG (Área de Conservación Guanacaste) project (Janzen & Hallwachs 2020). I started with the most common species in an attempt to affect the largest number of specimens in the ACG inventory databases. By describing these species, 1,943 specimens, or 12% of the entire phorid catch are being identified.

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Methods

Specimens were collected by Malaise traps in the surveys by Janzen and Hallwachs (2020) in northwestern Costa Rica. The sites and names for these four traps and their single year of trapping are as follows (more information on each site is given by Janzen and Hallwachs 2020):

BSE (2012-2013). Costa Rica: Área de Conservación Guanacaste, Guanacaste Province, Sector Santa Rosa, Bosque San Emilio, 10.84389 latitude, -85.61384 longitude, 300 m elevation. Dry forest (six months no rain and highly deciduous; six month rainy season). One-hundred-year-old secondary succession (the site was a banana plantation in mixed forest and pastures in 1920). Old growth forest is about 2 km away. There were 4,511 phorid specimens barcoded from this trap.

Derrumbe (2014-2015). Costa Rica: Área de Conservación Guanacaste, Guanacaste Province, near Estación Biológica Cacao; 10.92918 latitude, -85.46426 longitude, 1350 m, cloud forest understory, slight old landslide gap. Volcán Cacao is an isolated volcanic peak, not part of a mountain massif, but part of a Cordillera that ranges from 600 to 2000 m in different places (Volcán Orosi, Volcán Cacao, Volcán Rincon de la Vieja, Volcán Santa María). This forest has never been logged, but because of its slope, is periodically affected by narrow landslides. Rain year round, but in Dec-May, only sporadically. There were 3,408 phorid specimens barcoded from this trap.

ESG (2013-2014). Costa Rica: Área de Conservación Guanacaste, Alajuela Province, Sector San Cristobal, Estación Biológica San Gerardo; 10.88009 latitude, -85.38887 longitude, 575 m, mid-elevation Caribbean rain forest, maturing 100-year-old succession following long ago heavy logging, trap in sun on exact forest edge initially, but overgrown above by second year and lightly shaded, small stream about 5 m away. About 200 m from a small patch of original old-growth rainforest in one direction, unpaved road and cattle pasture in another direction. Rain year round but with seasonal intensity. 4,465 specimens.

Pailas II sites (Oct 2013-Oct 2014). Seven traps were run within a 2-3 km diameter ellipse centered on PL12 of ICE Geothermal Development Pailas II (Janzen & Hallwachs 2020), 750-850 m elevation, 10.76248 latitude, -85.33689 longitude. This forest lies exactly on the ecosystem join between mid-elevation rain forest and mid-elevation dry forest. Four-five months of quite dry weather but not dry enough for a deciduous forest. The vast majority, totaling 3,600 specimens (89% of the Pailas Dos specimens), were from trap PL12-3.

All specimens were individually DNA barcoded by Sanger sequencing in the Centre for Biodiversity Genomics in the University of Guelph, Guelph, Canada (http://ibol.org), and specimens assigned to BINs (Biodiversity Information Numbers) (Ratnasingham & Hebert 2013b). BINs were classified to genus based on the photographs published for each on the BOLD (Barcode of Life Database) website. Some remain unclassified to genus because photographs were insufficiently detailed to make a definite identification, whereas others represent possible new genera.

BINs, which are based on Refined Single Linkage Clustering Analysis (RESL) (Ratnasingham & Hebert 2013a) were used as starting points for species delimitation. To ensure that BINs were not oversplitting species, I examined photographs of the nearest neighbors of all BINs to ensure that they either differed noticeably in appearance or that they were separated by 3% or more minimum pairwise sequence divergence. Brown *et al.* (accepted) found that closely related *Megaselia* species in the *Megaselia sulphurizona* complex had interspecific divergences of as little as 1.5%, although most species differed by 2-8%, with most intraspecific distances below 1%. Hartop *et al.* (2021) recommended closer examination of clusters (=BINs in this paper) with divergence of 1.5% or greater, a number that would require greater scrutiny of about two-thirds of the species herein.

To further assess the similarity of barcodes and the variation within species, objective clustering (Meier *et al.* 2006) was also used, as implemented in SpeciesIdentifier (*taxondna.sourceforge.net*) with all specimens of the herein treated species on BOLD (Biodiversity of Life Datasystems).

To ensure that BINs were not overlumping species, I examined 10 representatives of each of the commonest (>100 specimens) *Megaselia* BINs to ensure that morphology-based species concepts were consistent with the barcodes, and to obtain both male and female specimens for imaging. Deep splits (2% or more intraspecific distances) within BINs were investigated by examination of specimens from each side of the split, if there were distinct clusters. In questionable cases, when intraspecific divergences were high and interspecific distances low, I requested a photograph of the most divergent specimen in the BIN to compare. Holotypes were selected from within the commonest haplotype in the BIN cluster, and its 658 bp barcode given (“-“ indicates missing data).

These measures to detect lumping and splitting are probably not sufficient in all instances to determine the correct species boundaries. Hartop *et al.* (2021) found, however, that the BOLD algorithm was about 86% correct in her data set, a number that is impressively high on its own. The procedures here will raise this success rate a further (but unknown) amount, and has the virtue of speeding the process considerably.

BINs that passed all of these checks were considered to be equivalent to species, and all specimens I examined were taken as the type series. To further document the specimens upon which these species were based, a set of FASTA files were deposited at the website www.phorid.net/data.

These species are also described from a reduced set of morphological characters based on the table-based descriptions initiated previously (Eiseman & Hartop 2015; Hartop & Brown 2014;2015; Hartop *et al.* 2015;2016). They are supplemented with photographs of the lateral habitus of a male, the dorsum of the female abdomen, the wing of a male, and the left side of the male terminalia for each species. Diagnoses consist of brief morphological comparison statements with nearest neighbors on BOLD, and of barcodes being within the BIN assignment. Minimum interspecific (Meier *et al.* 2008) and maximum intraspecific divergence differences from nearest neighbors of these barcodes are given for each species from SpeciesIdentifier.

Sample individual unique voucher codes from BOLD, with "BIOUG…" as the prefix for Malaise-trapped ACG specimens (in contrast to reared or otherwise collected) are given for holotypes and illustrated specimens to directly link their sequences to their specimens and information in BOLD, ACG and BioAlfa databases. Catalog numbers ("LACM…") are given for holotypes to facilitate their recognition. All material examined is listed in Supplementary Table 1. Holotypes are deposited in the Museo Nacional in Costa Rica (MNCR), with some other specimens in the insect collection of the Natural History Museum of Los Angeles County, but most are housed at the Center for Biodiversity Genomics, Guelph, Ontario, Canada.

TABLE 1. The most common phorid BINs in the dataset.

Number of specimens	BIN	Genus or species
892	BOLD:ACE6905	*Adenophora* sp.
707	BOLD:ACS9205 & ACF8681	*Megaselia normwoodleyi* **n. sp.**
408	BOLD:ADA8792	*Megaselia montywoodi* **n. sp.**
312	BOLD:ACE4575	*Physoptera* sp.
288	BOLD:ACT4414	*Metopina* sp.
226	BOLD:ACF9234	*Metopina*-group
217	BOLD:ACE8077	*Apocephalus* sp.
189	BOLD:ACF8680	*Metopina*-group
178	BOLD:ACS8553	new genus
157	BOLD:ABV9892	*Megaselia wendyporrasae* **n. sp.**
150	BOLD:ACS8139	*Apocephalus* sp.
133	BOLD:ACE9419	*Physoptera* sp.
130	BOLD:ABV9912	*Megaselia torbjornekremi* **n. sp.**
129	BOLD:ACS8802	*Metopina*-group
129	BOLD:ACS9233	*Metopina*-group
121	BOLD:ADF3571	*Megaselia thomaspapei* **n. sp.**
121	BOLD:AAU5568	*Apocephalus* sp.
115	BOLD:ADF3997	*Brownphora* sp.
114	BOLD:ABW1902	*Myriophora* sp.
114	BOLD:ADA8583	*Ceratusa* sp.
110	BOLD:ACU3726	*Apodicrania* sp.
108	BOLD:AAU5609	*Megaselia nealevenhuisi* **n. sp.**
107	BOLD:ACE0921	*Megaselia stevemarshalli* **n. sp.**
104	BOLD:ACF9051	*Apocephalus* sp.
103	BOLD:ACK9746	*Megaselia manuelzumbadoi* **n. sp.**
102	BOLD:ACE5745	*Megaselia artborkenti* **n. sp.**
100		

To minimize re-description of already known species, specimens were keyed using Borgmeier's keys to Neotropical species (Borgmeier 1958; 1962; 1969; 1971) and compared to other species descriptions published thereafter (reviewed by Hartop & Brown 2014). The chance of definitively morphologically identifying a small, brown, relatively featureless species (such as *Megaselia normwoodleyi* new species) is low, however. On the other hand, Borgmeier apparently enjoyed describing species based on females with unusual abdominal tergites, such as *M. manuelzumbadoi* new species (Fig. 10b) so it is likely that any species with such distinctive abdominal structure in our data set would have been named (if Borgmeier had seen them). Otherwise, we expect efforts linking our specimens to existing taxonomy to be unsuccessful unless the previously morphologically-discriminated holotypes can be DNA barcoded.

Etymologies were provided by Daniel Janzen, whose intention was to honor other dipterists involved in his inventory projects.

Results

Taxonomy of the most common *Megaselia* species

Species are treated in descending order of their abundance in trap samples.

Megaselia normwoodleyi new species

Figures 1a–c, 10.

Holotype: Male. BIOUG19594-F02, COSTA RICA: Alajuela: Sector San Cristobal, Estación San Gerardo, 10.88°N, 85.389°W, 575 m, 9.ix.2013, D. Janzen, W. Hallwachs, Malaise trap [LACM ENT 366335] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
ACCCTATATTTATTTTTGGTGCTTGAGCTGGAATAGTAGGAACTTCATTAAGAATTATAATTCGAGCCG
AATTAGGCCATCCTGGTGCACTAATTGGAGATGATCAAATTTATAATGTAATTGTCACAGCACATGCTT
TCATTATAATTTTTTTTATAGTTATACCTATTATAATAGGAGGATTTGGAAATTGATTAGTACCTTTAATAC
TTGGAGCTCCAGATATAGCATTTCCACGAATAAATAATATAAGATTTTGAATATTACCTCCATCTCTTAC
ACTTTTACTAGCCAGAAGTATAGTAGAAAATGGAGCTGGTACAGGATGAACTGTTTACCCTCCCCTAT
CTTCAAGAATCGCTCATAGTGGAGCTTCTGTCGATTTAGCAATTTTCTCTTTACATCTAGCAGGAATTT
CTTCTATTCTAGGAGCTGTAAATTTTATTACAACTATTATTAATATACGATCATCAGGTATTACATTTGAC
CGAATACCTTTATTTGTTTGATCAGTTGGAATTACAGCTCTACTACTTCTCTTATCTTTGCCAGTATTAG
CTGGTGCTATTACTATATTATTAACTGATCGAAACTTCAACACTTCT--------------------------------

Description. See Table 5. There are two BINs, BOLD:ACS9205 (which includes the holotype) and BOLD:ACF8681, that cannot be separated by morphology. Intense analysis, including wing venation morphometry (Brown and Wong, 2021), failed to find any confirming differences between these two BINs, although there is a minimum pairwise divergence of 2.13% between them (Table 6). In this situation, I recognized only one species, although I suspect that there are two. Until we know something about life histories of these flies, or have evidence from some other source, a division into two species cannot be justified.

Besides the barcodes, males of this species are distinctive by the enlarged medioventral single seta on both sides of the epandrium.

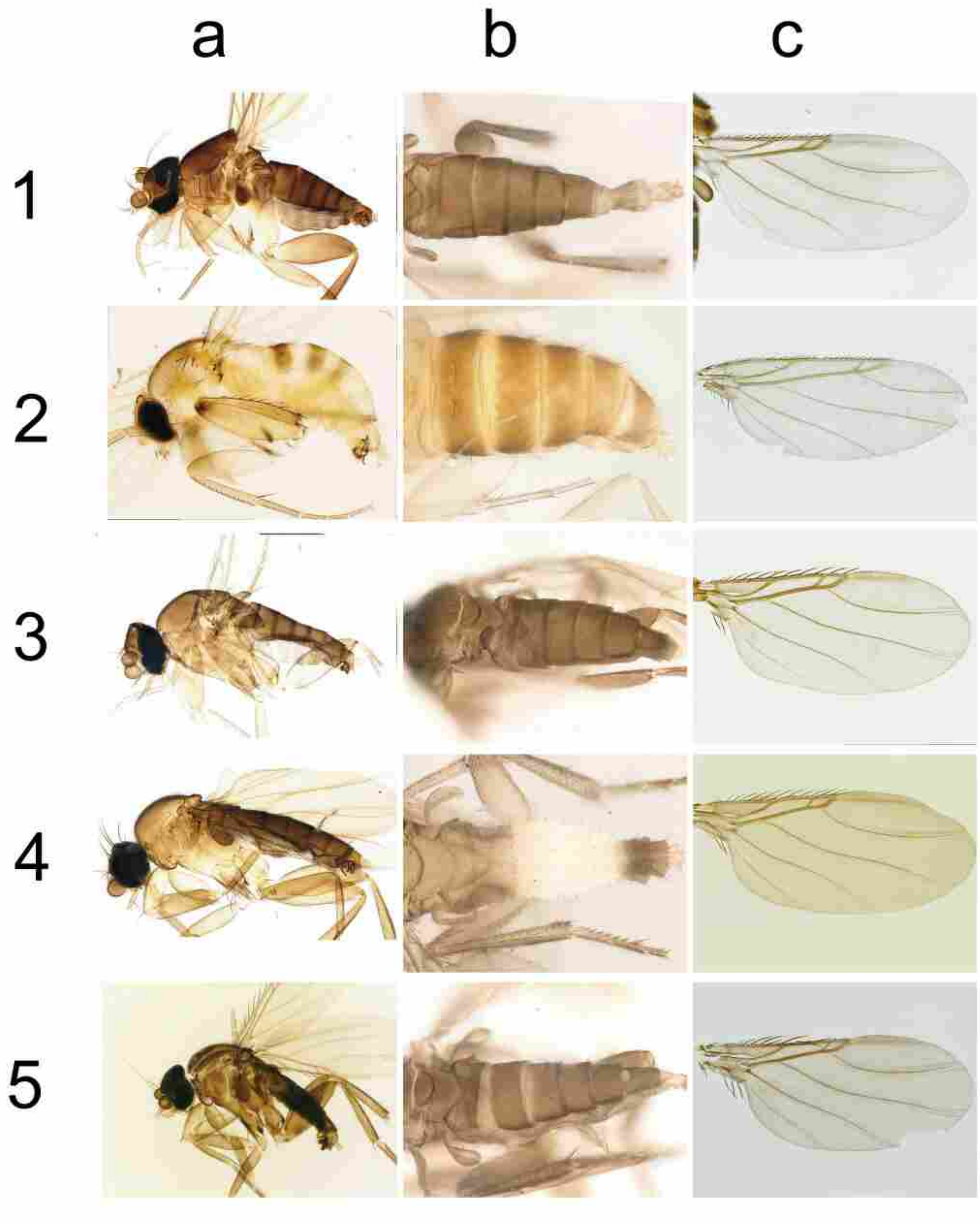
BIN: BOLD:ACS9205 and BOLD:ACF8681.

Distribution. This species was found almost exclusively at the ESG site.

Etymology. *Megaselia normwoodleyi* is named to honor Dr. Norman Woodley's unfailing decades at the Smithsonian/USDA of taxonomizing the thousands of ACG *Belvosia* (Tachinidae) reared for final identified deposition in the Canadian National Collection in Ottawa, cared for today by Mr. Alan Fleming.

Notes. With over 700 specimens, this was clearly the most common *Megaselia* species in the data set, but all specimens of BIN BOLD: ACS9205 were found only in the ESG (Caribbean rain forest) Malaise trap. The other

BIN, BOLD:ACF8681 is more widespread (found in all sites except Derrumbe), but still found mostly in the ESG trap.



FIGURES 1–5. *Megaselia* photographs. a, male habitus, left side; b, female abdomen, dorsal; c, male left wing. 1. *Megaselia normwoodleyi* **n. sp.**; 2, *Megaselia montywoodi* **n. sp.**; 3, *Megaselia wendyporrasae* **n. sp.**; 4, *Megaselia torbjornekremi* **n. sp.**; 5, *Megaselia thomaspapei* **n. sp.**.

In the clustering tree for BIN BOLD:ACS9205, there are two major groups of sequences separated by only one or two base pairs (.02%). Upon examination of specimens from each cluster, we find them to be morphologically indistinguishable, but experience with other species-rich taxa has located cases where two morphologically separable species differ by only 1–2 base pairs (e.g., Janzen *et al.* 2017). The potential for these two clusters to represent separate species can be investigated in the future with further genetic loci (Janzen *et al.* 2017).

Megaselia montywoodi new species

Figures 2a–c, 11.

Holotype: Male. BIOUG28603-F07, COSTA RICA: Guanacaste: Pailas II, PL12-1, 10.7642°N, 85.335°W, 828 m, 17.x.2013, D.Janzen, W.Hallwachs, Malaise trap [LACM ENT 366337] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
GGAATAGTAGGAACATCCTTAAGAATTTTAATCCGAGCTGAATTAGGACATCCAGGAGCCTTAATTGG
TGATGACCAAATTTATAATGTCATCGTAACTGCTCATGCATTTATTATAATTTTTTTATAGTTATACCTAT
TATAATAGGAGGATTTGGTAATTGACTAGTACCTCTAATATTAGGAGCCCCAGATATAGCATTCCCACGA
ATAAATAATATAAGATTCTGAATATTACCCCCTTCTTTAACTTTATTGTTAGCTAGAGGAATAGTAGATAA
TGGAGCTGGAACAGGCTGAACAGTTTATCCTCCTTTATCTTCCGGGATCGCTCATAGAGGAGCTTCTG
TTGATTTAGCAATTTTTTCTTTACATTTAGCTGGAATTTCTTCTATTCTTGGAGCAGTAAATTTTATTACT
ACCATTATTAATATACGATCACCAGGAATTTCCTTTGACCGAATGCCATTATTTATTTGATCTGTAAAAAT
TACAGCCATTCTTCTTCTTCTCTCATTGCCTGTATTAGCNGGAGNTATTACAATATTACTTACAGAC---

Description. See Table 5. The long costa (nearly .7 wing length), the complete row of anterodorsal setae on the midtibia and the shortened row on the hind tibia, along with the dome-shaped epandrium, are distinctive.

BIN:BOLD:ADA8792.

Distribution. Known only from the Pailas II sites in Costa Rica.

Etymology. *Megaselia montywoodi* is named to honor the late Dr. Monty Wood's 33 years of inspirational work at the Canadian National Collection in Ottawa for the rearing and taxonomizing of thousands of ACG Tachinidae and mentoring the study and taxonomy of the Tachinidae of Costa Rica through INBio and with Sr. Manuel Zumbado.

Notes. This species was only found in the Pailas II sites, and was strongly associated with Malaise trap PL 12-3A (330 out of 408 specimens). While this site is on the Pacific side of ACG, it lies exactly on the ecosystem join between Costa Rican dry forest (e.g., BSE site) and the Caribbean rain forest side of ACG, where the rain forest wraps around Volcan Rincon de la Vieja and therefore is contiguous with ESG rain forest.

The closest BIN is BOLD:ACW5562, a species of similar appearance found only at the ESG (Caribbean forest) site, but which differs by a minimum pairwise distance of over 5% (Table 6).

Megaselia wendyporrasae new species

Figures 3a–c, 12.

Holotype: Male. BIOUG31512-B08, COSTA RICA: Guanacaste: Derrumbe, 10.9292°N, 85.4643°W, 1220 m, 6.xi.2014, Malaise trap, D. Janzen and W. Hallwachs [LACM ENT 366283] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
ATTTTTGGAGCATGAGCTGGAATAGTAGGTACTTCATTAAGTATCATAATTCGAGCTGAATTAGGTCAC
CCAGGTGCTTTAATTGGAGATGATCAAATTTATAATGTAATTGTTACCGCTCACGCTTTTATTATAATTTT
TTTTATAGTTATACCAATTATAATAGGAGGATTTGGAAATTGATTAGTCCCTTTAATACTTGGAGCTCCA
GATATAGCTTTTCCACGAATAAATAATATAAGATTCTGATTATTACCCCCATCATTAACTTTACTATTGGC

TAGAAGTATAGTAGAAAACGGAGCTGGAACTGGATGAACAGTTTACCCTCCTCTTTCATCAAGAATTG
CCCATAGTGGGGCTTCTGTAGATTTAGCTATTTTTTCATTACACCTAGCAGGAGTGTCATCAATTTTAG
GAGCAGTAAATTTTATCACTACTATTATTAATATACGATCTTTAGGAATCACTTTTGATCGAATGCCCTTA
TTTGTTTGATCAGTAGGAATTACTGCTTTATTACTTTTACTTTCCTTACCTGTTTTAGCCGGAGCAATTA
CTATGTTATTAACAGAT-------------------------------------

Description. See Table 5. The long, thin, posterior apex of the epandrium is distinctive in this species.

BIN:BOLD:ABV9892.

Distribution. Known exclusively from the Derrumbe site in Costa Rica.

Etymology. *Megaselia wendyporrasae* is named to honor Costa Rican biologist Wendy Porras, who has worked with me for many years on Phoridae.

Notes. The closest BIN to *M. wendyporrasae* is BOLD:ADF8175, known from 8 specimens from the Derrumbe site. It differs from *M. wendyporrasae* by 3.10%, but the photo of the specimen on BOLD is not detailed enough to determine how similar it is to *M. wendyporrasae*. I will examine them, however, when revising the rest of the ACG *Megaselia*.

Megaselia torbjornekremi **new species**

Figures 4a–c, 13.

Holotype: Male. BIOUG31709-B12, COSTA RICA: Guanacaste: Derrumbe, 10.9292°N, 85.4643°W, 1220 m, 22.i.2015, D. Janzen and W. Hallwachs [LACM ENT 366332] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
TACATTATATTTTATTTTTGGAGCTTGAGCTGGAATAGTAGGTACTTCTTTAAGTATTATAATTCGAGCTG
AATTAGGACACCCTGGTGCTTTAATTGGTGATGACCAAATTTATAATGTAATTGTTACTGCCCATGCTTT
TATTATAATTTTTTTTATAGTAATACCTATTATAATAGGAGGATTTGGTAATTGACTAGTTCCTTTAATATT
AGGAGCTCCTGATATAGCTTTTCCTCGAATAAATAATATAAGTTTTTGAATATTACCTCCTTCTTTAACT
CTTTTATTAGCCAGAAGTATAGTAGAAAACGGAGCTGGAACTGGGTGAACAGTTTATCCTCCTCTTTC
TTCAAGTATTGCCCATAGTGGGGCTTCTGTTGATTTAGCAATTTTCTCATTACATTTAGCAGGAATTTCA
TCAATTCTAGGGGCTGTAAATTTTATTACAACTATTATTAATATACGATCTTCAGGTATTACATTTGATCG
AATACCTTTATTTGTTTGATCAGTAGGAATTACTGCTCTTTTATTACTTTTATCTTTACCAGTATTAGCCG
GAGCTATTACTATACTTTTAACGGATCGA----------------------------------

Description. See Table 5. This female of this species is highly distinctive due to its bright white abdominal segments 3–6. Tergites 3–6 are transparent, although their outline is still visible, and appear white. Also distinctive are the complete, strong subcosta, ending in vein R_1 and the minute hypoproct setae in males.

BIN: BOLD:ABV9912.

Distribution. Known only from the Derrumbe site in Costa Rica.

Etymology. *Megaselia torbjornekremi* is named to honor Dr. Torbjorn Ekrem of the NTNU University Museum in Norway for his eager and high quality administrative and science participation in the iBOL international meetings in South Africa and in Trondheim, Norway, and especially in support of BioAlfa and the ACG-ICE project to biomonitor the Pailas II geothermal site.

Notes. The closest BIN to *Megaselia torbjornekremi*, is BOLD:ADF6080, which differs by a minimum of 3.95% and is also known only from the Derrumbe site. The structure of the female abdomen in this species, although similar to that of *M. torbjornekremi*, is different, however, and it is clearly a different species. In particular, females of BOLD:ADF6080 are larger, and have the abdomen brown instead of bright white. Males are closely similar.

The bright white abdomen in females of this species is strongly indicative of female mating display and sexual role reversal (Brown & Porras 2015; Cumming 1994; Sivinski 1988). In species with this type of mating, we expect females to have more distinctive characters that are sexually selected, unlike the usual situation with species that have more distinctive characters in the male genitalia. Thus it is not surprising that males of *M. torbjornekremi* are similar to those of BOLD:ADF6080, whereas females differ.

TABLE 5. Descriptions of *Megaselia* species.Abbreviations are given in Hartop & Brown (2014). ? = unknown or unable to observe.

species	*normwoodleyi*	*montywoodi*	*wendyporrasae*	*torbjornekremi*
Borgmeier group	VII	I	IV	VII
supra-antennal setae	2 unequal	1	2 unequal	2 unequal
VIF position	close to eye	mid	close to eye	slightly closer to eye
SPS vesicles	few	none	none	none
palpus	yellow	yellow	yellow	yellow
labellar spinosity	no	no	no	no
anepisternal setation	bare	hairs plus enlarged setae	hairs	bare
# npl setae	3	3	3	2
npl cleft	no	no	no	no
scutellar setae	2	4	2	2
HT costal index	0.5	0.69	0.55	0.49
HT CSR	3.5: 2.0	2.5:3.6	2.5:2.2	2.6:1.9
sc	faint, incomplete	short, complete	incomplete	complete
alular setae	2	6	2	3
halter color	same (brown)	same (yellow)	darker	darker
epandrial setae (LS)	1 large ventral bristle-like seta at midlength	none enlarged	small	small
AT	short	long	long	short
hypandrium	with short process	with short process	with narrow process	process short, broad
female abdomen	unmodified	unmodified	unmodified	abdominal segments 3–6 white, including tergites; contrasting strongly with brown segments 1–2, and 7–10.
other notable features		midtibia with anterodorsal setal row; hind tibia with 2 anterodorsal setae near base only	epandrium posteriorly narrowed apex	hypoproct setae minute

......continued on the next page

TABLE 5. (Continued)

species	*thomaspapei*	*nealevenhuisi*	*stevemarshalli*	*manuelzumbadoi*	*artborkenti*
Borgmeier group	IV	VII–VIII	VII	I	VII
supra-antennal setae	2 unequal	2 unequal	1	2 unequal	2 unequal
VIF position	closer to eye	closer to eye	slightly closer to mid	close to eye	close to eye
SPS vesicles	none	few	none	none	none
palpus	brown	yellow	brown	brown	yellow
labellar spinosity	?	few (thin)	few	dense	no
anepisternal setation	hairs	bare	bare	hairs plus one slightly differentiated bristle	bare
# npl setae	3	3	2	3	3
npl cleft	no	no	no	no	no
scutellar setae	2	2	2	4	2
HT costal index	0.54	0.44	0.57	0.53	0.45
HT CSR	3.0:2.6	3.3: 1.9	4.0:4.1	3.7:2.9	2.5:1
sc	complete	faint, incomplete	short, incomplete	short, faint	faint, incomplete
alular setae	3	?	3	3	?
halter color	darker	darker	darker	lighter	darker
epandrial setae (LS)	1 large ventral at midlength	1 large ventral at midlength	long but thin	small	2 large on ventral margin near midlength
AT	long	short	long	long	medium
hypandrium	with long thin process	with short process	without processes	with narrow left process	with short left process
female abdomen	unmodified	unmodified	tergites 4 and 5 reduced, smaller than tergite 6. Female abdomen laterally with dense, fine setulae.	tergites 2–3 enlarged, brown, rest of abdomen reduced, yellow.	
other notable features	wing strongly brown-tinged	hypoproct setae minute	epandrium truncate; posterior margin of venter of segment six with row of long thicker setae		cercus loop present

Megaselia thomaspapei new species

Figures 5a–c, 14.

Holotype: Male. BIOUG31689-C11, COSTA RICA: Guanacaste: Derrumbe, 10.9292°N, 85.4643°W, 1220 m, 8.i.2015, D. Janzen and W. Hallwachs [LACM ENT 366331] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
ACATTATACTTCATTTTTGGAGCATGAGCTGGAATAGTAGGAACTTCTTTAAGTATTATAATTCGAGCTG
AATTAGGTCACCCAGGTGCCTTAATTGGGGATGACCAAATTTATAATGTAATTGTAACTGCTCACGCTT
TTATTATAATTTTTTTTATAGTAATACCTATTATAATAGGAGGGTTTGGTAATTGATTAGTACCCTTAATAC
TTGGAGCTCCAGATATAGCTTTCCCTCGAATAAATAATATAAGATTCTGGTTACTACCTCCATCACTAAC
TCTTTTATTAGCAAGAAGTATAGTAGAAAACGGAGCTGGAACTGGATGAACAGTTTATCCTCCCCTTT
CATCTAGTATTGCTCATAGAGGAGCTTCTGTAGATTTAGCAATTTTCTCTCTACATTTAGCAGGAATTTC
CTCAATTCTAGGAGCTGTAAATTTTATTACAACTATTATTAATATACGTTCTTCAGGAATTACTTTTGATC
GAATACCTTTATTTGTGTGGTCTGTAGGAATCACTGCTTTACTTCTTTTATTATCACTTCCTGTTTTAGC
AGGAGCAATTACTATACTATTAACAGATCGA------------------------------

Description. See Table 5. This species has a notably darkened wing, complete R_1, and long costal setae. The left side of the epandrium ends in a distinctive small clear lobe.

BIN BOLD:ADF3571.

Distribution. Known only from the Derrumbe site in Costa Rica.

Etymology. *Megaselia thomaspapei* is named to honor Dr. Thomas Pape of the Natural History Museum of Denmark for his eager and enthusiastic contributions to Costa Rican Sarcophagidae taxonomy for ACG, INBio/MNCR and now BioAlfa.

Notes. The maximum intraspecific divergence in this species, at 2.72% (Table 6), is greater than most; examination of specimens from different haplotypes show no significant differences, however. It is well-separated at over 7% divergence from the closest BIN, BOLD:ABW6434, known from a single specimen from French Guiana.

Megaselia nealevenhuisi new species

Figures 6a–c, 15.

Holotype: Male. BIOUG07689-H03, COSTA RICA: Guanacaste: Bosque San Emilio, 10.8438°N, 85.6138°W, 300 m, 23.iv.2012, D. Janzen, Malaise trap [LACM ENT 366336] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
AACTTTATACTTTATTTTTGGGGCTTGAGCTGGTATAGTAGGAACCTCTTTAAGAATTATAATTCGAGCA
GAATTAGGGCATCCTGGAGCTTTAATTGGTGATGATCAAATTTATAATGTAATTGTTACTGCCCATGCTT
TTATTATAATTTTCTTTATAGTAATACCTATTATAATAGGAGGGTTCGGAAATTGACTAGTACCTTTAATA
CTTGGAGCTCCTGATATGGCTTTTCCTCGAATAAATAACATAAGATTTTGGATATTACCTCCATCTCTCA
CCTTATTGTTAGCAAGAAGAATAGTGGAAAATGGGGCCGGGACAGGTTGAACTGTTTACCCTCCTTTA
TCTTCTAGAATTGCCCATAGAGGGGCTTCAGTTGACTTAGCAATTTTCTCCTTACATCTTGCAGGTATC
TCATCTATCTTAGGGGCTGTAAATTTTATTACAACAATTATTAATATACGATCTTCAGGAATTTCTTTCGA
CCGAATGCCTTTATTTGTTTGATCAGTTGGAATTACAGCTCTATTATTACTATTATCATTACCTGTTCTAG
CAGGTGCTATCACCATACTATTAACAGATCGAAATTTTAATACTTCATTTTTTGACCCTGCTGGAGGAG
GAGATCCAATTCTCTATCAACATTTATTT

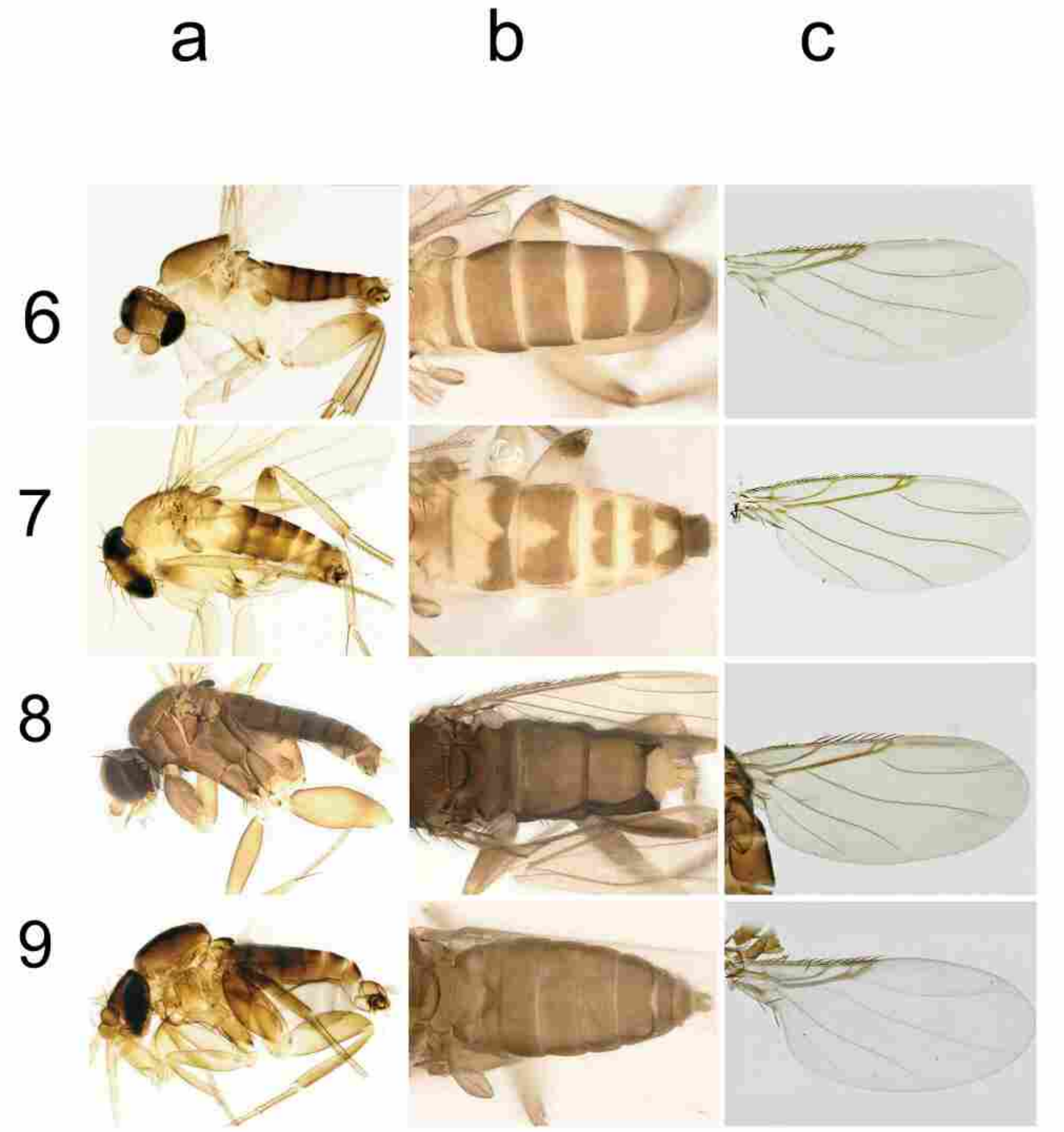
Description. See Table 5. The epandrium is short and square-shaped, and there is a distinctive short cercus and hypoproct.

BIN: BOLD:AAU5609**.**

Distribution. This BIN is known from Belize, Costa Rica, and Mexico.

Etymology. *Megaselia nealevenhuisi* is named to honor Dr. Neal Evenhuis of the Bishop Museum, Hawaii, for his eager and enthusiastic contributions to Costa Rican Bombyliidae taxonomy for ACG, INBio/MNCR and now BioAlfa.

Notes. This species is found in 3 of the 4 sites (missing from the Derrumbe site), but over one-half of the specimens are from the BSE site; otherwise four specimens were collected from ESG, and 25 from Pailas II. The most similar BIN is BOLD:ABA8279, which differs by a minimum of over 10%, is bright yellow in color, and is found in Canada.



FIGURES 6–9. *Megaselia* photographs. a, male habitus, left side; b, female abdomen, dorsal; c, male left wing.; 6, *Megaselia nealevenhuisi* **n. sp.**; 7, *Megaselia stevemarshalli* **n. sp.**; 8, *Megaselia manuelzumbadoi* **n. sp.** ; 9, *Megaselia artborkenti* **n. sp.**

Megaselia stevemarshalli new species

Figures 7a–c, 16, 19, 22, 25.

Holotype: Male. BIOUG05283-A06, COSTA RICA: Guanacaste: Bosque San Emilio, 10.8438°N, 85.6138°W, 300 m, 4.vii. 2012, D. Janzen, Malaise trap [LACM ENT 366330] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
AACTTTATATTTATTTTTGGAGCCTGAGCAGGAATAGTAGGAACTTCATTAAGAATCATAATTCGAGC
TGAACTTGGACATCCTGGTGCTTTAATTGGTGATGATCAAATTTACAATGTAATTGTAACTGCCCATGC
TTTTATTATAATTTTTTTTATAGTTATACCTATTATAATAGGTGGATTTGGGAATTGATTAGTCCCTTTGAT
ATTAGGAGCTCCTGATATAGCTTTCCCTCGAATAAATAATATAAGTTTTTGAATACTTCCTCCTTCTTTA
ACATTATTATTAGCCAGCAGTATAGTCGAAAATGGAGCTGGAACAGGATGAACTGTTTATCCTCCTCTC
TCGTCTAGAATTGCTCATAGTGGTGCTTCTGTAGATTTAGCCATTTTTTCTCTCCATTTAGCTGGTATTT
CTTCAATTTTAGGAGCAGTAAATTTTATTACTACAATTATTAATATGCGATCAACAGGTATTACATTTGAT
CGTATACCTTTATTTGTATGATCTGTAGGAATTACAGCTATTCTTCTTTTACTTTCTCTTCCTGTTTTAGC
TGGAGCTATTACTATACTTCTAACAGATCGAAATTTTAACACTTCATTTTTTGATCCTGCTGGTGGGGG
AGATCCTATTCTTTATCAACATTTATTT

Description. See Table 5. This light-colored species has a long costa with short costal setae, and a broad yellow cercus. Females have tergites with contrasting light and dark markings and dense lateral abdominal setae.

BIN: BOLD:ACE0921.

Distribution. Known from two Pacific slope sites in Costa Rica, most common at BSE (99 specimens versus 8 from Pailas II).

Etymology. *Megaselia stevemarshalli* is named to honor Dr. Steve Marshall of the University of Guelph, Canada, for his eager and enthusiastic taxonomic and sociological contributions to the Diptera of the world and his instructive fly photographs decorating many museum walls.

Notes. The closest BIN is BOLD:ADB7997, which differs by a minimum of 2.92%, (one specimen only; all the rest differ by over 3%) and is represented by only a few specimens from Pailas II. The nearest neighbor of that BIN is BOLD: ACE0920, with a minimum distance of 1.4% . All three are similar in appearance, but closer examination of specimens of the other two BINs showed some consistent differences (Figs. 19–27). Males of *M. stevemarshalli* (Fig. 25) lack the thick epandrial setae of the other two species (Figs. 26–27). Females of BOLD:ADB7997 (Fig. 23) have about twice the setal density on the dorsum of the abdomen as the females of *M. stevemarshalli* (Fig. 22) and BOLD:ACE0920 (Fig. 24), whereas the latter also has the shape of tergite 4 (Figs. 21, 24) differing greatly from the other two (Figs. 19, 20, 22–23).

***Megaselia manuelzumbadoi* new species**

Figures 8a–c, 17.

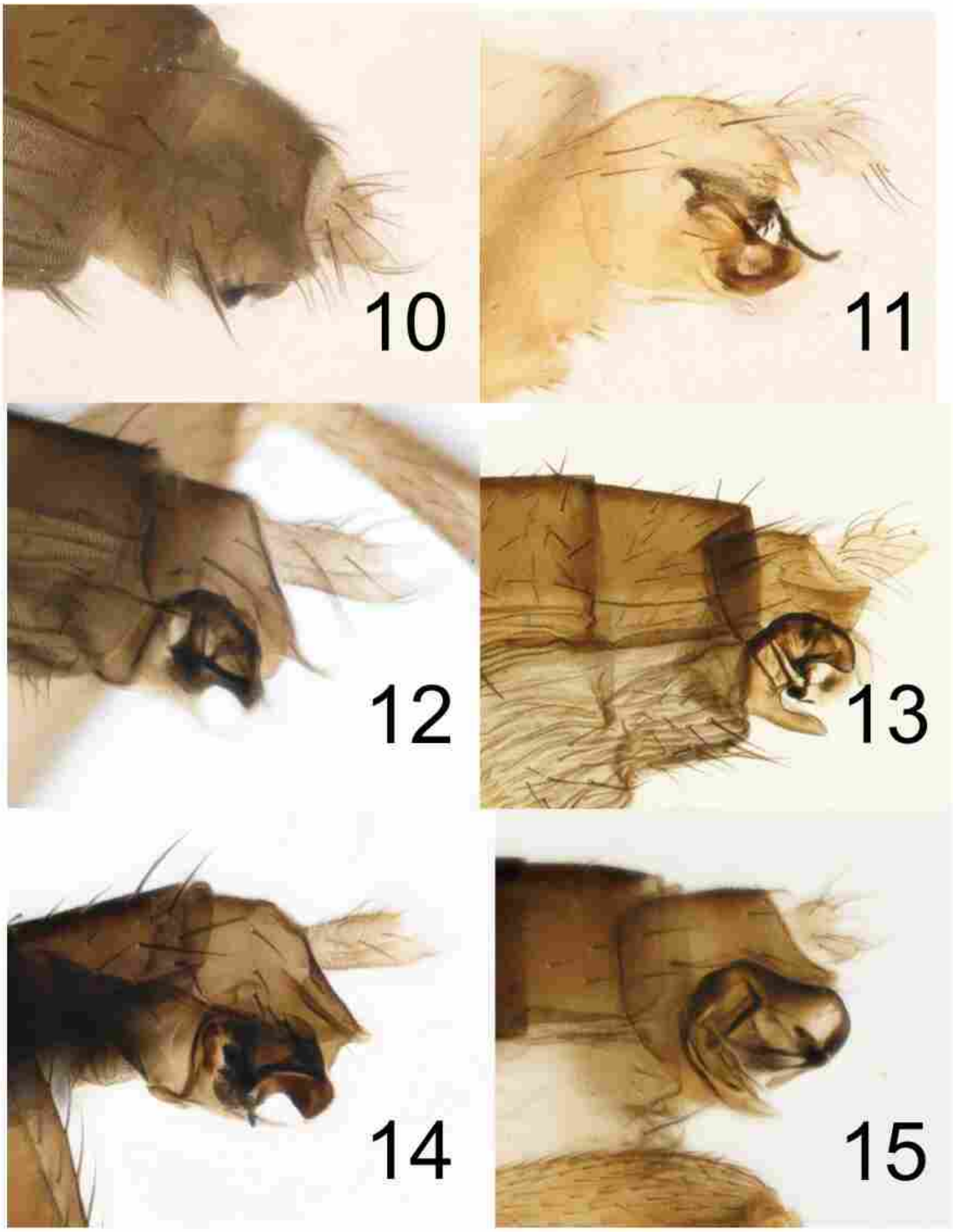
Holotype: Male. BIOUG30012-G05, COSTA RICA: Guanacaste: Pailas II, PL12-3, 10.76431N, 85.3344°W, 820 m, 2.x.2014, D.Janzen, W.Hallwachs, Malaise trap [LACM ENT366301] (MNCR).

Paratypes: See Supplementary Table 1.

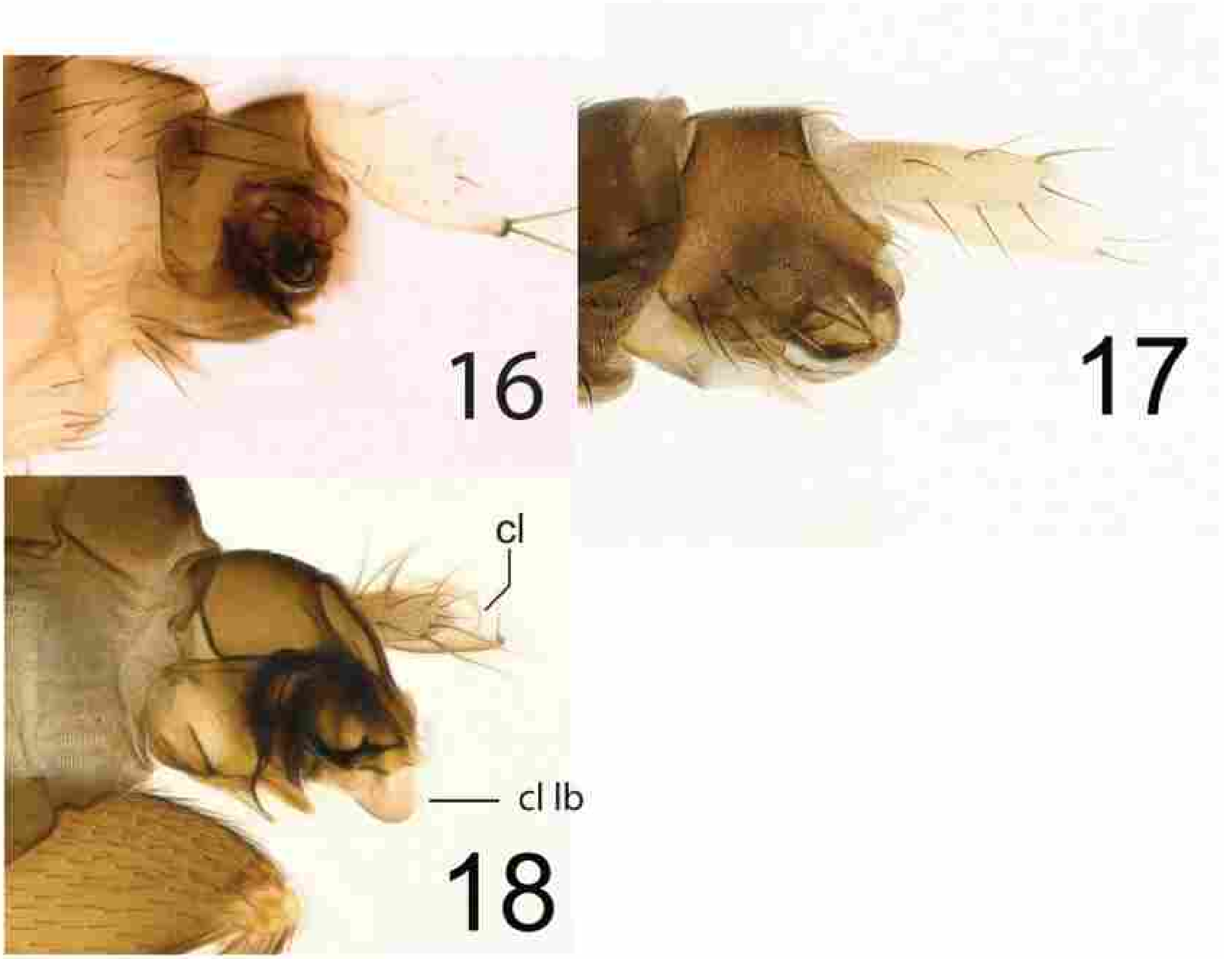
Description. See Table 5.

Holotype barcode:
ACATTATATTTATTTTTGGAGCATGAGCGGGTATAGTAGGAACATCACTTAGTATTATAATTCGAGCTG
AATTAGGTCATCCAGGTGCCTTAATTGGAGATGATCAAATTTATAATGTAATTGTAACTGCTCATGCATT
TATCATAATTTTTTTTATAGTAATACCTATTATAATAGGAGGATTTGGTAATTGATTAGTCCCATTAATATT
AGGAGCACCAGATATGGCATTTCCTCGTATAAATAATATAAGATTTTGAATATTACCCCCATCATTAACA
CTATTGTTAGCCAGAAGCATAGTAGAAAATGGAGCTGGGACAGGATGAACAGTGTACCCCCCCTTATC
ATCTAGAATTGCACATAGTGGAGCTTCAGTAGATTTAGCAATTTTTTCTCTTCATTTAGCTGGAATTTCT
TCTATTCTAGGAGCAGTAAATTTTATTACTACCATTATTAATATACGATCATCAGGTATTACTTTTGATCG
TATACCTTTATTTGTTTGATCAGTAGGAATTACTGCTCTATTACTTTTATTATCTTTACCAGTATTAGCTG
GAGCTATTACTATACTTTTAACAGATCGA

Distribution. Known from Argentina, Colombia, and Costa Rica, based on records in BOLD. Specimens morphologically identified as the similar species *Megaselia luteicauda* (Borgmeier) are much more widely recorded, from as far north as the southern USA (Barnes 1991) and from islands in the Caribbean Sea (e.g. Borgmeier 1969). At least some of these are probably other species (including BOLD:AAG3298, discussed below). In the ACG samples, *M. manuelzumbadoi* was strongly associated with the PL12-3 site at Pailas II (almost 90% of specimens), but I have seen morphologically similar specimens from other sites in Costa Rica.



FIGURES 10–15. Male terminalia of *Megaselia* species, left lateral. 10, *Megaselia normwoodleyi* **n. sp.**; 11, *Megaselia montywoodi* **n. sp.**; 12, *Megaselia wendyporrasae* **n. sp.**; 13, *Megaselia torbjornekremi* **n. sp.**, 14, *Megaselia thomaspapei* **n. sp.**; 15, *Megaselia nealevenhuisi* **n. sp.**



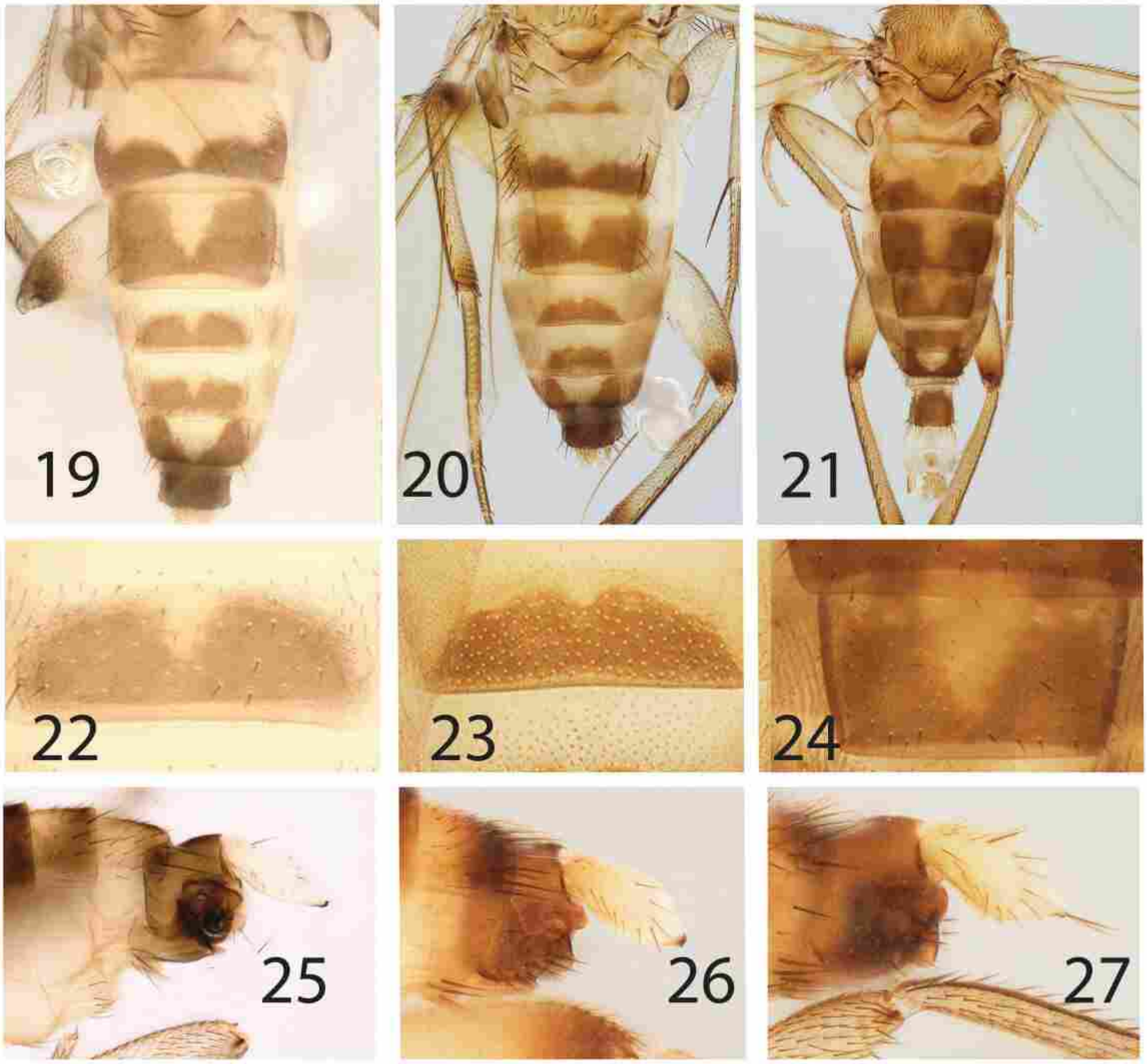
FIGURES 16–18. Male terminalia of *Megaselia* species, left lateral. 16, *Megaselia stevemarshalli* **n. sp.**; 17, *Megaselia manuelzumbado* **n. sp.** ; 18, *Megaselia artborkenti* **n. sp.**, 20. Abbreviations: cl – cercus loop; cl lb – clear lobe.

BIN: BOLD:ACK9746.

Natural History. Borgmeier (1969) mentioned that a specimen of *M. luteicauda* from Argentina was collected feeding on a dead opilionid; we know nothing about the specificity of this association, however, and whether dead opilionids represent a potential breeding host for this species. Many phorids apparently are attracted to dead invertebrates just to feed.

The bright yellow apex of the abdomen in females of this species is strongly indicative of female mating display and sexual role reversal (Brown & Porras 2015; Sivinski 1988).

Notes. This species is similar to *Megaselia luteicauda* (Borgmeier), described from Petrópolis, Rio de Janeiro, Brazil. Until the holotype of *M. luteicauda* can be barcoded, however, it seems unwise to assume they are the same species. Furthermore, the closest BIN is BOLD:AAG3298, which differs by only 1.35%. It is widely distributed among the ACG sites, except Derrumbe. It also has a highly modified female abdomen, although slightly different in details from that of *Megaselia manuelzumbadoi*, in that the lighter color is more extensive in BOLD:AAG3298. Specimens of BOLD:AAG3298 are known from two clusters from the southern USA and these ACG samples respectively, separated from each other at 1.30%. Given that there are closely similar variants of "yellow-tailed *Megaselia*", until we have more material from more places, we will not be able to assess whether the pattern is one of continuous differences, or of multiple cryptic species.



FIGURES 19–26. Details of species similar to *Megaselia stevemarshalli* new species. Figs. 19–21. Female abdomen, dorsal. Fig. 19 *M. stevemarshalli* new species. 20, BIN BOLD:ADB7997. 21, BIN BOLD:ACE0920.Figs. 22–24. Details of female tergite 5. Fig. 22, *M. stevemarshalli* new species. 23, BIN BOLD:ADB7997. 24, BIN BOLD:ACE0920. Figs. 25–27. Male terminalia, left lateral. Fig. 25. *M. stevemarshalli* new species. 26, BIN BOLD:ADB7997. 27, BIN BOLD:ACE0920.

***Megaselia artborkenti* new species**

Figures 9a–c, 18.

Holotype. Male. BIOUG05406-G08, COSTA RICA: Guanacaste: Bosque San Emilio, 10.8438°N, 85.6138°W, 300 m, 16.vii.2012, D. Janzen, Malaise trap [LACM ENT 366307] (MNCR).

Paratypes: See Supplementary Table 1.

Holotype barcode:
CACATTATATTTATATTTGGGGCCTGAGCAGGTATAGTAGGAACCTCCTTAAGAATTATAATTCGTGCT
GAACTAGGTCATCCGGGCGCTTTAATTGGAGATGACCAAATTTATAACGTAATTGTAACTGCACATGCT
TTTATTATAATTTTTTTATAGTAATACCTATTATAATAGGAGGATTCGGCAACTGACTTGTCCCTTTAAT
ACTGGGAGCTCCAGATATGGCTTTCCCTCGAATAAATAATATAAGTTTTTGAATACTCCCTCCTTCCTT

GACATTATTATTAGCCAGAAGCATAGTAGAAAATGGGGCAGGAACCGGTTGAACTGTTTATCCTCCTTTATCCTCTAATATTGCCCATAGTGGTGCATCTGTTGACCTAGCAATTTTTTCTCTTCATTTAGCAGGTATCTCTTCTATTCTAGGAGCAGTAAATTTTATCACTACAATCATTAACATACGAACAACAGGAATTACCTATGACCGAATGCCCTTATTTGTCTGATCTGTGGGAATTACGGCCCTCCTTTTATTACTCTCTCTACCTGTATTAGCAGGAGCAATTACAATACTACTTACTGACCGAAACTTTAATACTTCATTTTTTGATCCTTCAGGAGGAGGAGACC

Description. See Table 5. In lateral view, this species has a flat, disk-shaped structure over the cerci (a cercus loop), as do a number of other species described by Hartop *et al.* (2015): *M. marquezi, francoae,* and *carthayensis,* as well as those of the *M. sulphurizona* complex (Brown *et al.* accepted). It differs from the sympatric and otherwise similar *M. carthayensis* by apex of the right side of the epandrium, which has a large clear lobe in *M. artborkenti* (Fig. 18) that is not found in *M. carthayensis*. They also differ by the barcode, which is highly divergent (minimum differences are in the 17–20% range).

BIN: BOLD:ACE5745.

Distribution. Widespread; known from Argentina, Costa Rica, Honduras, and Mexico based on DNA barcodes in BOLD.

Etymology. *Megaselia artborkenti* is named to honor Dr. Art Borkent, the Canadian world authority on Ceratopogonidae flies for his enthusiastic embracing of efforts to understand whole Diptera faunas and for sharing his knowledge of biting flies.

Notes. This species was found at the BSE and Pailas sites II. The closest species in BOLD to this one is BOLD: ADK2686, which differs by a minimum of 5.13%, and is represented by two specimens from the Derrumbe site.

TABLE 6. Percent divergence for new *Megaselia* species and their nearest neighbors in BOLD. All divergences calculated using SpeciesIdentifier.

Species	Mean interspecific	Minimum interspecific	Maximum intraspecific
normwoodleyi	3.02	2.13	1.14
montywoodi	6.04	5.76	2.34
wendyporrasae	3.54	3.10	1.59
torbjornekremi	4.60	3.95	1.69
thomaspapei	7.64	7.31	2.72
nealevenhuisi	10.89	10.54	1.95
stevemarshalli	3.21	2.90	0.92
manuelzumbadoi	1.71	1.52	1.84
artborkenti	5.40	5.13	1.73

Discussion

Taxonomy. The BOLD algorithm was successful in classifying species in in all cases except for one pair of BINs that showed no morphological differences. The two BINs comprising *M. normwoodleyi* have 2.4% mean interspecific divergence and relatively low intraspecific divergence. In other organisms, information about host plants (in butterflies) and parasitoid hosts (of parasitic wasps) provide an additional data source to support decisions to recognize one species or many. For example, BINs that contain two or more clusters of barcodes of morphologically identical species might be found to have different hosts in the same place at the same time. Unfortunately, we have no such information for the species of *Megaselia* treated herein, and the recognition of separate species would have to be justified on the basis of percent barcode divergence alone. More study of this species hopefully can take place in the future.

There is a wider range of divergences among and within species treated herein than in our previous work on the *Megaselia sulphurizona* complex (Brown *et al.* accepted). This is to be expected, however, given that the *M. sulphurizona* complex represented only one lineage, whereas those in the current paper are from varied, apparently unrelated groups. Presumably, some of these different groups are of different ages, and so are more or less divergent than others.

It is important that both sexes should be examined when deciding on species limits in *Megaselia*, especially in the tropics. There, sexual role reversal is more common than in temperate regions, judging from illustrations in Borgmeier (1962) of many species with reduced female abdominal tergites that facilitate expansion of membranous structures to appear more attractive to mates (Brown & Porras 2015). In such species, we expect females, rather than the males, to have the more distinctive and diagnostic character states.

Although the species described here are not part of a revision, some interesting distributional information was obtained. Some species, such as *M. artborkenti* and its nearest neighbor, are found on the Pacific slope, but one in the lowlands, the other at higher elevation. This is a pattern common among many other taxa be found by the inventory (D.H. Janzen, personal communication). Also, it is evident that some phorids have strong site (and habitat) fidelity, with five common species represented by specimens from only one site (*M. wendyporrasae, torbjornekremi*, and *thomaspapei* from Derrumbe, almost all *M. normwoodleyi* from ESG, and *M. montywoodi* from Pailas II). Clearly, our understanding of the limits of the extent of these distributions would greatly benefit from barcoding specimens from further sites in the Neotropical Region as well as more simply and feasibly, across Costa Rica.

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