RESEARCH ARTICLE



New records of an alien aphid species *Tinocallis* (*Sappocallis*) *takachihoensis* from countries in central and northern Europe (Hemiptera, Aphididae, Calaphidinae)

Mariusz Kanturski¹, Yerim Lee², Łukasz Depa¹

I Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia in Katowice, Bankowa 9, 40–007 Katowice, Poland 2 Laboratory of Insect Biosystematics, Department of Agricultural Biotechnology, Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul, Republic of Korea

Corresponding author: Mariusz Kanturski (mariusz.kanturski@us.edu.pl)

Academic editor: R. Blackman Received 13 October 2017 Accepted 15 December 2017 1	Published 17 January 2018

Citation: Kanturski M, Lee Y, Depa Ł (2018) New records of an alien aphid species *Tinocallis* (*Sappocallis*) *takachihoensis* from countries in central and northern Europe (Hemiptera, Aphididae, Calaphidinae). ZooKeys 730: 1–17. https://doi.org/10.3897/zookeys.730.21599

Abstract

The aphid genus *Tinocallis* Matsumura, 1919 (Hemiptera: Aphididae: Calaphidinae) in central and northern Europe is reviewed; it includes four species. The first records of the Asian elm aphid *Tinocallis takachihoensis* Higuchi, 1972 are reported from the Czech Republic, Denmark, and Poland. The record in Denmark is the first in Scandinavia. Alate viviparous females and nymphs of *T. takachihoensis* were collected from *Ulmus glabra* "Pendula" (the Czech Republic and Poland) and from *U. minor* (Denmark) in 2017. *Tinocallis takachihoensis* is the fourth *Tinocallis* species to be recorded from Poland and together with two other species from the subgenus *Sappocallis*, *T. nevskyi* and *T. saltans*, is a species of alien origin. The alate viviparous females are reviewed and re-described and their affinities and distribution in central and northern Europe are discussed. A key to the European species of *Tinocallis* based on the characters of live and slide-mounted specimens is also given.

Keywords

Aphidoidea, distribution, new record, Sternorrhyncha, Ulmus glabra 'Pendula'

Introduction

Of the approximately 1590 aphid species described or recorded from Europe (Nieto Nafría et al. 2013) to date, approximately 103 species are known to be of an alien origin from North America and Asia (Coeur d'acier et al. 2010, Pérez Hidalgo et al. 2011; Rakauskas 2011; Panini et al. 2017). The area of Poland is one of the best recognised in terms of aphid fauna in Europe with 766 recorded species and subspecies (Wojciechowski et al. 2015; Kanturski et al. 2017) to date. In Poland, as many as 34 species of an alien origin were reported earlier (Wieczorek 2011). However, this number is continuously changing due to ongoing research and biological invasions (Kanturski et al. 2017; Walczak et al. 2017).

The aphid genus *Tinocallis* Matsumura, 1919 (Calaphidinae) comprises 18–19 species within four subgenera (Favret 2017; Lee and Lee 2017) and is the second largest *Panaphidini* genus (Quednau 2001; Favret 2017). The species of this genus are characterised by a small and delicate body and are mostly associated with Ulmaceae (Blackman and Eastop 1994, 2017). All of the viviparae are alate and they usually have paired spinal and marginal tubercular processes on the thorax and abdomen. The secondary rhinaria on antennal segment III are narrow, transversely elongated, or slit-like. The genus has caused many taxonomical difficulties due to its seasonal variations (Quednau 2001).

The Asian elm aphid, *Tinocallis takachihoensis* Higuchi, 1972, is one of the members of the subgenus *Sappocallis* Matsumura, 1919. This species was originally described from Japan and is known to be primarily distributed in Eastern Asia (Higuchi 1972). *Tinocallis takachihoensis* along with *T. saltans* (Nevsky, 1929), *T. ulmiparvifoliae* Matsumura, 1919, and *T. zelkowae* (Takahashi, 1919) have been introduced to other parts of the world (Blackman and Eastop 2017; Foottit et al. 2006; Quednau and Shaposhnikov 1988). In Europe, this species was reported for the first time from France (from a suction trap) (Leclant 1986). Since then, this species has been reported from the United Kingdom (Döring 2007, 2008) and the Mediterranean area (Patti and Barbagallo 1997; Mier Durante and Perez Hidalgo 2002; Barbagallo and Massimino Cocuzza 2014). Although recent observations of the occurrence of this species come from Greece (Papapanagiotou et al. 2012), Germany, and the Netherlands (Piron 2013), Piron's information comes from a personal communication from Schrameyer who received the name of the species in question from Thieme (T. Thieme, pers. comm.).

In this paper, the occurrence of *T. takachihoensis* from the Czech Republic, Denmark, and Poland is reported for the first time. Its affinities to other known *Tinocallis* species from these regions are also discussed and a morphological key to the identification of all European representatives of this genus is provided.

Material and methods

Alate viviparous females and nymphs of *Tinocallis takachihoensis* were collected in Opava (the Czech Republic) on 19.08.2017, Katowice (Poland) on 12.07.2017, and Copenha-

gen (Denmark) on 16.06.2017. The aphids were transferred to 80% ethanol and prepared after the Kanturski and Wieczorek (2012) protocol. In-life photographs were taken by the Sony SLT digital camera with the Sigma EX 50 mm lens with intermediate rings. Mounted specimens were examined by a Nikon Eclipse E600 and photographed by Nikon DS-Fi camera. The slides are deposited in the Aphidoidea collection of the Department of Zoology, University of Silesia in Katowice, Poland (UŚ).

The following abbreviations are used:

BL	body length;		
HW	greatest head width across compound eyes;		
ANT	antennae or their lengths;		
ANT I, II, III, I	V, V, VI antennal segments I, II, III, IV, V, VI or their lengths (ratios		
	between antennal segments are simply given as e.g. 'VI: III');		
BASE	basal part of last antennal segment or its length;		
РТ	processus terminalis of last antennal segment or its length;		
URS	ultimate segments of rostrum (IV + V) or their length;		
Cu _{1a}	first cubital vein;		
Cu _{1b}	second cubital vein;		
FEMORA III	hind femora length;		
TIBIAE III	hind tibiae length;		
HT I	first segment of hind tarsus,		
HT II	second segment of hind tarsus or its length;		
SIPH	siphunculi or their length.		

For morphological comparison slides of *Tinocallis* specimens from other localities were used. The studied material is deposited in the Natural History Museum in London, UK (**BMNH**), and Zoological Institute, Polish Academy of Sciences, Warsaw, Poland (**ZMPA**).

Taxonomy

Genus *Tinocallis* Matsumura, 1919 Figs 1–8

Tinocallis Matsumura, 1919: 100. *Lutaphis* Shinji, 1924: 346.

Diagnosis. This genus can be recognized by having narrow transversely elongated or slit-like secondary rhinaria on ANT III, and ABD III, V, and VII with laterally displaced spinal dorsal setae. Abdominal tergites I and II usually have finger-like dorsal tubercles.

Type species. Tinocallis ulmiparvifoliae Matsumura, 1919.

Tinocallis (Sappocallis) takachihoensis Higuchi, 1972

Figs 1-8; Table 1

Redescription. Alate viviparous female

Colour. Colour of live specimens: head and thorax black, ANT pale yellow with dark apices of segments, fore and middle legs pale vellow, hind legs pale vellow with black distal part of femora and proximal part of tibiae. Wings pigmented on the area of pterostigma, media and Cu₁₁. Abdomen yellow (Fig. 1a, c). Pigmentation of mounted specimens: head and thorax brown (Fig. 1a). ANT pale with brown ANT I and ANT II and slightly darker apices of flagellar segments (Fig. 2a). Morphometric characters. ANT 0.76–1.00 × BL and 0.26–0.27 × HW. ANT III with 17–21 slit-like secondary rhinaria (Fig. 3a). PT 1.13–1.19 × BASE. Other antennal ratios: ANT VI/ANT III 0.57-0.64, ANT V/ANT III 0.52-0.54, ANT IV/ANT III 0.52-0.61. Ant I with 3 setae, Ant II with 2-3, ANT III with 9-13 setae, ANT IV with 2 setae, ANT V with 2-3 setae, ANT VI with one basal seta. URS 0.18 × ANT III, 0.28-0.32 × ANT VI, and $0.90-1.00 \times HT$ II. Pronotum with two finger-like projections on the distal part (Fig. 4a). Mesonotum with two large, imbricated projections with rounded apices (Fig. 5a). HT II 0.18–0.20 × ANT III and 0.31–0.32 × ANT VI. Forewings with distal branches of media bordered with fuscous and with more-or-less extensive fuscous patches at distal ends of Cu_{1a} and Cu_{1b} (Fig. 6a). Hind legs with dark distal part of femora and proximal part of tibiae (Fig. 7a). Abdomen pale, SIPH pale on basal part and pale brown on apex. Abdomen without sclerotisation besides very small darker projections on ABD III-V (Fig. 8a).

Material examined. Six alate viviparous females, CZECH REPUBLIC: Moravskoslezský kraj (Opava and vicinity), 18 Aug 2017, No. 08/17/5, on *Ulmus glabra*, coll. M. Kanturski (UŚ); five alate viviparous females, **DENMARK**: North East Zealand (Copenhagen), 18 Jun 2017, No. 05/17/3, on *Ulmus* sp., coll. M. Kanturski (UŚ); 15 alate viviparous females, **POLAND**: Upper Silesia (Katowice), 12 Jul 2017, No. 07/172b, on *Ulmus glabra* 'Pendula', coll. M. Kanturski (UŚ).

Additional material examined. six alate viviparous females, CHINA: Xiangshan Botanic Garden, 25 May1985, No. VFE18142, RLB3615, on *Ulmus* sp., coll. R. Blackmam & V. Eastop (BMNH); three alate viviparous females, UNITED KINGDOM: Humberside, 16 Oct 1997, No. BM1999–7 on *Zelkova serrata*, coll. not known (BMNH).

Tinocallis (Eotinocallis) platani (Kaltenbach, 1843)

Figs 1-8; Table 1

Redescription. Alate viviparous female

Colour. Colour of live specimens: head and prothorax yellow with brown longitudinal stripes. The rest of thorax brown. ANT pale yellow with dark apices of segments, fore and middle legs pale yellow, hind legs with black femora and proximal part of

Character	T. takachihoensis	T. platani	T. saltans	T. nevskyi
Character	n = 20	n = 13	n = 9	n = 15
BL	1.27–1.47	1.75-2.25	1.50-1.75	1.72-1.90
HW	0.39–0.46	0.45-0.46	0.40-0.45	0.40-0.42
ANT	1.48–1.73	1.65-1.77	1.06-1.35	1.34–1.48
ANT III	0.50-0.59	0.60-0.70	0.38-0.49	0.45-0.47
ANT IV	0.26-0.36	0.36-0.39	0.21-2.28	0.27-0.30
ANT V	0.27-0.31	0.31-0.32	0.17-0.22	0.22-0.28
ANT VI	0.32-0.34	0.21-0.22	0.19-0.23	0.29-0.32
BASE	0.15	0.17-0.18	0.10-0.12	0.14
PT	0.17-0.18	0.04	0.09-0.11	0.15-0.18
URS	0.09-0.11	0.12-0.13	0.05-0.06	0.085
III FEMUR	0.38-0.58	0.48-0.58	0.36-0.40	0.43-0.45
III TIBIA	0.74–1.06	1.00-1.20	0.63-0.70	0.74-0.79
HT I	0.03-0.04	0.04-0.05	0.03	0.02-0.03
HT II	0.10-0.11	0.11-0.12	0.10	0.09
Forewings	1.82-2.50	2.25-2.75	1.75-2.00	2.05-2.25
Hind wings	1.00-1.80	1.37-1.75	1.20-1.55	1.25–1.37
SIPH	0.04-0.05	0.07-0.10	0.05-0.06	0.03-0.04
cauda length	0.05-0.06	0.07-0.08	0.07	0.05
cauda width	0.05-0.06	0.06-0.08	0.05-0.07	0.06
genital plate length	0.07-0.08	0.09-0.10	0.08-0.09	0.07-0.08
genital plate width	0.12-0.15	0.17-0.20	0.11-0.12	0.13-0.18

Table 1. Measurements (in mm) of alate viviparous females of *Tinocallis* species studied.

tibiae. Wings pigmented on the area of pterostigma, media and Cu_{1b} . Abdomen yellow with brown extensive spots on the dorsal side (Fig. 1b). Nymphs pale yellow (Fig. 1d). Pigmentation of mounted specimens: head and thorax brown. ANT pale with brown ANT I, ANT II and slightly darker apices of flagellar segments (Fig. 2b).

Morphometric characters. ANT 0.78–0.94 × BL and 0.25–0.27 × HW. ANT III with 16–26 slit-like secondary rhinaria (Fig. 3b). PT 0.23–0.25 × BASE. Other antennal ratios: ANT VI/ANT III 0.31–0.35, ANT V/ANT III 0.45–0.51, ANT IV/ANT III 0.55–0.60. Ant I with 3–4 setae, Ant II with 4, ANT III with 10–15 setae, ANT IV with 3–5 setae, ANT V with 2–4 setae, ANT VI with one basal seta. URS 0.18–0.20 × ANT III, 0.57 × ANT VI, and 1.04–1.09 × HT II. Pronotum without projections. Only very small protuberances, similar to those on the head are visible (Fig. 4b). Mesonotum without projections (Fig. 5b). HT II 0.17–0.18 × ANT III and 0.52–0.55 × ANT VI. Forewings without a radial sector. Stigma and media strongly bordered with fuscous basally as well as distally, with a dark spot over Cu_{1b} (Fig. 6b). Hind legs with uniformly dark brown femora and proximal part of tibiae (Fig. 7b). Abdomen robust, pale with brown more or less extensive dorsal sclerites or broken crossbars. SIPH dark brown (Fig. 8b).

Material examined. three alate viviparous females, GERMANY: Lehmen, 18 Aug 1936, No. BM1984–340, on *Ulmus effusa* (= *U. laevis*), coll. D. Hille Ris Lambers (BMNH); three alate viviparous females, POLAND: Piekary Śląskie, 19 May 2015,



Figure 1. Live specimens of **a** *Tinocallis takachihoensis* **b** *T. platani* **c** *T. takachihoensis* with first instar larvae **d** larvae and nymphs of *T. platani* **e** *T. saltans* **f** *T. nevskyi*.

No. 04/15/33 on *Ulmus* sp., coll. M. Kanturski & Ł. Depa (UŚ); three alate viviparous females, Warszawa, 13 May 1962, No. R3953, on *Ulmus laevis*, coll. H. Szelegiewicz (ZMPA); four alate viviparous females, UNITED KINGDOM: London, Kew, 29 Jun 1965, No. BM1982–492, on *Ulmus laevis*, coll. H.L.G Stroyan (BMNH).

Tinocallis (Sappocallis) saltans (Nevsky, 1929)

Figs 1-3; 5-8; Table 1

Redescription. Alate viviparous female.



Figure 2. Mounted specimens of alate viviparous females of **a** *Tinocallis takachihoensis* **b** *T. platani* **c** *T. saltans* **d** *T. nevskyi.*

Colour. Colour of live specimens: head brown, ANT yellow with distinctly darker apices of ANT IV and V and almost whole ANT VI. Prothorax yellow or light brown, the rest of thorax dark brown to dark brown. Legs pale with visible darker distal part of hind femora. Abdomen yellow with brown with brown, small and rounded sclerites (Fig. 1e). Pigmentation of mounted specimens: head and thorax light brown to brown with lighter prothorax. The rest of body pale (Fig. 2c).

Morphometric characters. ANT 0.71–0.77 × BL and 0.33–0.37 × HW. ANT III with 12–17 transverse oval secondary rhinaria (Fig. 3c). PT 0.95 × BASE. Other antennal ratios: ANT VI/ANT III 0.47–0.51, ANT V/ANT III 0.44, ANT IV/ANT III 0.55–0.57. Ant I with 3 setae, Ant II with 2, ANT III with 10–11 setae, ANT IV with 2–4 setae, ANT V with 2 setae, ANT VI with one basal seta. URS 0.10–0.15 × ANT III, 0.21–0.30 × ANT VI, and 0.50–0.60 × HT II. Pronotum with four projections, two on distal and two on proximal part (Fig. 4c). Mesonotum with two small, imbricated projections on the distal part with rounded apices (Fig. 5c). HT II 0.20–0.26 × ANT III and 0.42–0.51 × ANT VI. Forewings with base of pterostigma with dark spot and pigmentation or bordering on branches of media and delicate light brown spot near Cu_{1b} (Fig. 6c). Hind legs pale or light brown with darker distal part of femora



Figure 3. Antennae of alate viviparous females of **a** *Tinocallis takachihoensis* **b** *T. platani* **c** *T. saltans* **d** *T. nevskyi*.

(Fig. 7c). Abdomen pale with brown sclerites with distinct tubercles on ABD III-V. SIPH brown (Fig. 8c).

Material examined. three alate viviparous females, CHINA: Xiangshan, 25 May 1985, No. VFE 18128, on *Ulmus* sp., coll. V.F. Eastop (BMNH); two alate viviparous females POLAND: Katowice, 17 Jul 2016, No. 07/16/10, on *Ulmus* sp., coll. M. Kanturski leg., UŚ; two alate viviparous females, TAJIKISTAN: Gissarskij cgrebt (1300m), 03 Jul 1959, No. R.3964, on *Ulmus campestris*, coll. M. Narzikulov (ZMPA); two alate viviparous females, UKRAINE: Kanevskij zapov., 17 Aug 1945, No. R.3961, on *Ulmus* sp., coll. V. Mamontova (ZMPA).

Tinocallis (Sappocallis) nevskyi Remaudière, Quednau & Heie, 1988 Figs 1–8; Table 1

Redescription. Alate viviparous female

Colour. Colour of live specimens: whole body pale yellow to whitish yellow with poorly visible very small, brown abdominal sclerites. Wings not pigmented (Fig. 1f).



Figure 4. Head and pronotum features **a** pronotum of *Tinocallis takachihoensis* with one pair of projections (black arrowheads) **b** head and pronotum of *T. platani* without projections (arrows) **c** pronotum of *T. nevskyi* with two pairs of projections.



Figure 5. Mesonotum of a *Tinocallis takachihoensis* b *T. platani* (without projections) c *T. saltans* d *T. nevskyi*.

Pigmentation of mounted specimens: head pale with light brown edges, ANT pale, pronotum pale with light brown longitudinal stripes. The rest of thorax brown (Fig. 2d).

Morphometric characters. ANT 0.78 × BL and 0.28–0.29 × HW. ANT III with 13–15 slit-like secondary rhinaria (Fig. 3d). PT 1.07–1.24 × BASE. Other antennal ratios: ANT VI/ANT III 0.64–0.69, ANT V/ANT III 0.50–0.59, ANT IV/ANT III 0.60–0.63. ANT I with 2–3 setae, ANT II with 2, ANT III with 7–10 setae, ANT IV with 2–3 setae, ANT VI with one basal seta. URS 0.18 × ANT III, 0.26–0.29 × ANT VI, and 0.09–0.94 × HT II. Pronotum with four projections, two on distal and two on proximal part (Fig. 4c). Mesonotum with two large and wide basally, imbricated projections on the distal part (Fig. 5d). HT II 0.20 × ANT III and 0.29–0.31 × ANT VI. Forewings with apices of media and Cu_{1a} with very small, poorly visible spots (Fig. 6d). Hind legs pale with small dark spot on distal part of femora, but the end of femora also pale (Fig. 7d). Abdomen, pale with brown, very small dorsal sclerites on ABD III-VIII but those on ABD VII and VIII poorly visible. SIPH pale brown (Fig. 8d).

Material examined. three alate viviparous females, AFGHANISTAN: Kabul, 08 May 1975, No. BM 1984–340, on *Ulmus* sp., coll. R. van den Bosch (BMNH); four alate viviparous females, POLAND: Katowice (first record for Upper Silesia),



Figure 6. Forewing pigmentation of a *Tinocallis takachihoensis* b *T. platani* c *T. saltans* d *T. nevskyi*.



Figure 7. Hind leg pigmentation of a Tinocallis takachihoensis b T. platani c T. saltans d T. nevskyi.

12 Jul 2017, No. 07/17/2a, on *Ulmus glabra* 'Pendula', coll. Kanturski (UŚ); two alate viviparous females, SWEDEN: Lund, 03 Sep 1978, No. R.3963, on *Ulmus glabra*, coll. R. Danielsson (UŚ); six alate viviparous females, UNITED KINGDOM: ex culture of G. Hopkins, 04 Oct 1995, No. RLB 4337, on *Ulmus* sp., coll. R. Blackman (BMNH).



Figure 8. Abdominal sclerotization of Central and North European *Tinocallis*: **a** *T. takachihoensis* **b** *T. platani* **c** *T. saltans* **d** *T. nevskyi*.

Key to the species of the genus *Tinocallis* in Europe

1	Live specimens: head and thorax yellow or brown, abdomen yellow with or without brown patches. Mounted specimens: head and pronotum without projections (Fig. 4b). Mesonotum without projections. PT shorter than 0.50 × BASE
_	Live specimens: head and thorax from yellow to dark. If brown to dark, then abdomen only with small circular sclerites and scleroites. Mounted speci- mens: pronotum with one or two pairs of finger-like projections (Figs. 4a, c). Mesonotum with one pair of projections. PT as long as or longer than 0.50 × BASE
2	Live specimens: head and thorax brown, abdomen yellow with extensive brown patches (Fig. 1b). Mounted specimens: forewings pigmented, hind femora brown, abdomen with extensive, dark sclerotisation (Fig. 2b)
_	Live specimens: pale yellow without any patches. Mounted specimens: forewings not pigmented, hind femora pale, abdomen without dark sclerotisation
3	Live specimens: head and thorax black, abdomen yellow without dark scler- ites (Fig. 1a, c). Pronotum with one pair of projections on distal part. Fore- wings pigmented. Hind legs with brown distal part of femora and proximal part of tibiae (Fig. 7a)
_	Live specimens: head and thorax greenish or yellow to brown, abdomen with small to large circular sclerites or marginal projections. Mounted specimens: pronotum with two pairs of projections on proximal and distal part. Fore- wings pigmented or not pigmented. Hind legs with pale femora only with a brown spot or band on the distal part and pale tibiae (Fig. 7c, d)
4	Live specimens: greenish or bluish-green. Mounted specimens: Head with all projections prominent, the distal pair almost as long as the projections on the pronotum. Marginal projections on ABD II-IV almost as long as the spinal projections
_	Live specimens: yellow to brown. Mounted specimens: Head with small pro- jections, the distal pair clearly shorter than projections on pronotum. Mar- ginal projections on ABD II-IV clearly shorter than spinal projections 5
5	Live specimens: head and thorax brown, abdomen with clearly visible scler- ites with projections or tubercles, wings clearly pigmented (Fig. 1e). Mounted specimens: ANT III secondary rhinaria transverse oval (Fig. 3c). Wings clear- ly pigmented. Abdomen with small, sclerotised, spinal projections on ABD IV (Fig. 8c)
_	Live specimens: head and thorax yellow or thorax brown with poorly visible sclerites, wings not pigmented. Mounted specimens: ANT III secondary rhinaria slit-like (Fig. 3d). Wings very poorly pigmented. Abdomen without small sclerotised spinal projections on ABD IV (with only two sclerites) (Fig. 8d)

Distribution comments

Of the approximately 18 valid *Tinocallis* species, six are known from Europe (Blackman and Eastop 2017). Although Nieto Nafría et al. (2013) also include Sarucallis kahawaluokalani (Kirkaldy, 1906) as a representative of *Tinocallis* (in the subgenus Sarucallis), we follow the full generic status of Sarucallis (Quednau 2003). Two of the Tinocallis species known from Europe, T. ulmiparvifoliae and T. zelkowae, are only known from south-western Europe and on bonsai trees imported into the United Kingdom, while the remaining taxa have been reported to occur more widely, especially in central and northern Europe. From the four species presented here, T. platani is characterised as being widely distributed, T. nevskyi in the central, western, and northern parts of the continent, while *T. saltans* is recorded mostly in the central and eastern parts of Europe, but also from Italy and Spain (Nieto Nafría and Mier Durante 1998). Earliest European records of *T. takachihoensis* were from southern France and Italy, with more recent records from Greece, Germany, Malta, and the Netherlands. Thus, it seems from the dispersion routes of this species in Europe, that for more than a decade it has preferred regions with milder climate (the Mediterranean Basin and the western coast of Europe). Its sexual generation is as yet only known from Malta (Patti and Barbagallo 1997). The recent finding in Central Europe indicates the possibility of either the overwintering of this species in the climatic conditions of this part of Europe or rapid early-summer migrations from the territory that is already occupied (Piron 2013). Despite some milder winters, which have occurred in Central Europe recently and have influenced aphid biology (Depa et al. 2015), the period of aphid collection in this case (June-August) indicates the second possibility. The species, however, requires observation as it may become a pest on ornamental plants or it may adapt to more severe climatic conditions.

Acknowledgements

The first author is extremely grateful to Henrik Enghoff and Jan Pedersen (Natural History Museum of Denmark, University of Copenhagen, Denmark) for their kind help and support during his internship in the Museum. This research (DK-TAF 6818) received support from the SYNTHESYS Project, which is financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Programme.

We would like to thank Thomas Thieme, Nicolás Pérez Hidalgo and Roger Blackman for all comments and suggestions that improved the first version of the manuscript.

References

- Barbagallo S, Massimino Cocuzza GE (2014) A survey of the aphid fauna in the Italian regions of Latium and Campania. Redia XCVII: 19–47.
- Blackman RL, Eastop VF (1994) Aphids on the Worlds Trees. An Identification and Information Guide. CAB International, Wallingford, 987 pp.

- Blackman RL, Eastop VF (2017) Aphids of the World's Plants: An Online Identification and Information Guide. http://www.aphidsonworldsplants.info [Accessed 25.08. 2017]
- Coeur d'acier A, Pérez Hidalgo NP, Petrović-Obradović O (2010) Aphids (Hemiptera, Aphididae) Chapter 9.2. In: Roques A, Kenis M, Lees D, Lopez-Vaamonde W, Rabitsch W, Rasplus JY, Roy DB (Eds) Alien Terrestrial Arthropods of Europe BioRisk 4 (Special Issue): 435–474. https://doi.org/10.3897/biorisk.4.57
- Depa Ł, Taszakowski A, Kanturski M (2015) Impact of warm weather events on prolongation of the life cycle of *Stomaphis* Walker (Hemiptera, Aphididae, Lachninae). Turkish Journal of Zoology 39: 669–671. https://doi.org/10.3906/zoo-1404–6
- Döring TF (2007) Colonies of the Asian elm aphid *Tinocallis takachihoensis* Higuchi (Hemiptera: Aphididae) in Britain. The Entomologist's record and Journal of Variation 119(5): 226–227.
- Döring TF (2008) Further sightings of the Asian elm aphid *Tinocallis takachihoensis* Higuchi (Hemiptera: Aphididae) in Britain. The Entomologist's record and Journal of Variation 120: 32.
- Favret C (2017) Aphid Species File. Version 5.0/5.0. http://Aphid.SpeciesFile.org [25.08.2017]
- Foottit RG, Halbert SE, Miller GL, Maw E, Russell LM (2006) Adventive aphids (Hemiptera: Aphididae) of America north of Mexico. Proceedings of the Entomological Society of Washington 108: 583–610.
- Higuchi H (1972) A taxonomic study the subfamily Callipterinae in Japan (Homoptera: Aphididae). Insecta Matsumura 35: 19–126.
- Leclant F (1986) Cultures ornementales. Le puceron du *Lagerstroemia*, nouveau ravageur pour notre flore. Phytoma Défense des cultures: 49–50.
- Lee Y, Lee S (2017) A review of the *Tinocallis* Matsumura (Hemiptera: Aphididae) on the Korean peninsula, with description of one new species. Journal of Asia Pacific Entomology 23(3): 1019–1031. https://doi.org/10.1016/j.aspen.2017.07.005
- Kanturski M, Wieczorek K (2012) Metody zbioru i preparowania mszyc (Hemiptera, Aphidoidea) w badaniach faunistycznych, taksonomicznych i molekularnych. Młodzi Naukowcy dla Polskiej Nauki 8(V): 137–143.
- Kanturski M, Mruk K, Morawski M, Wojciechowski W, Depa Ł (2017) Nearctaphis bakeri (Cowen, 1895) and Illinoia liriodendri (Monell, 1879) – two aphid species (Hemiptera: Aphididae) of alien origin new to the Polish fauna. Annals of The Upper Silesian Museum in Bytom. Entomology 26 (online 002): 1–6.
- Matsumura S (1919) New species and genera of Callipterinae (Aphididae) of Japan. Transactions of the Sapporo Natural History Society 7: 99–115.
- Mier Durante MP, Pérez Hidalgo N (2002) Dos especies de Panaphidini (Hemiptera, Aphididae, Calaphidinae), propias de árboles ornamentales, introducidas en la Península Ibérica. Boletim da Sociedade Portugesa de Entomologia 157 (Supl. 6): 213–217.
- Nieto Nafría JM, Mier Durante MP (1998) Hemiptera, Aphididae I. Fauna Iberica 11: 1-424.
- Nieto Nafría JM, Andreev AV, Binazzi A, Mier Durante MP, Pérez Hidalgo N, Rakauskas R, Stekolshchikov A (2013) Fauna Europaea: Aphidoidea. Fauna Europaea version 2.6.2. www.faunaeur.org [accessed 25.08 2017]
- Panini M, Massimino Cocuzza G, Dradi D, Chiesa O, Mazzoni E (2017) First report of *Myzus mumecola* (Matsumura, 1917) in Europe. Bulletin OEPP/EPPO Bulletin 47(1): 107–110. https://doi.org/10.1111/epp.12357

- Papapanagiotou AP, Nathanailidou M, Taylor M, Zarpas KD, Voudsouris K, Tsitsipis JA, Margaritopoulos JT (2012) New records of aphid species (Hemiptera: Aphididae) in Greece. Entomologia Hellenica 21: 54–68. https://doi.org/10.12681/eh.11518
- Patti I, Barbagallo S (1997) Recenti acquisizioni faunistiche sugli Afidi della Sicilia. Bollettino del Laboratorio di Entomologia agraria Filippo Silvestri 53: 29–84.
- Pérez Hidalgo N, Umaran A, Mier Durante MP (2011) First record of the adventive oriental aphid *Schizaphis piricola* (Matsumura, 1917) (Hemiptera, Aphididae) in Europe. ZooKeys 89: 49–56. https://doi.org/10.3897/zookeys.89.903
- Piron PGM (2013) Appearance of *Tinocallis takachihoensis* (Homoptera: Aphididae) in The Netherlands. Entomologische berichten 73(6): 251–252.
- Quednau FW (2001) World review of the genus *Tinocallis* (Hemiptera: Aphididae, Calaphidinae) with description of a new species. The Canadian Entomologist 133: 197–213. https:// doi.org/10.4039/Ent133197–2
- Quednau FW (2003) Atlas of the Drepanosiphine aphids of the world part II: Panaphidini Oestlund, 1923-Panaphidina Oestrund, 1923 (Hemiptera: Aphidinae: Calaphidinae). The American Entomological Institute, Florida, 301 pp.
- Quednau FW, Shaposhnikov GCh (1988) A list of Drepanosiphine aphids from the Soviet Far East, with descriptions of new species (Homoptera: Aphidoidea). The Canadian Entomologist 120(11): 1017–1032. https://doi.org/10.4039/Ent1201017–11
- Rakauskas R (2011) Aphid species (Hemiptera, Sternorrhyncha: Aphididae) alien and invasive to Lithuania. Aphids and other Hemipterous Insects 17: 21–27.
- Shinji O (1924) New aphids from Morioka. Dobutsugaku 36: 343-373. [In Japanese]
- Walczak U, Borowiak-Sobkowiak B, Wilkaniec B (2017) Tetraneura (Tetraneurella) nigriabdominalis (Hemiptera: Aphidoidea) – a species extending its range in Europe, and morphological comparison Tetraneura (Tetraneura) ulmi. Entomologica Fennica 28: 21–26.
- Wieczorek K (2011) Aphid species alien to Poland (Hemiptera: Aphididae). Polish Journal of Entomology 80: 203–224. https://doi.org/10.2478/v10200–011–0015–2
- Wojciechowski W, Depa Ł, Kanturski M, Węgierek P, Wieczorek K (2015) An annotated checklist of the Aphids (Hemiptera: Aphidomorpha) of Poland. Polish Journal of Entomology 84: 383–420. https://doi.org/10.1515/pjen-2015–0033

CHECKLIST



A global checklist of the 932 fruit fly species in the tribe Dacini (Diptera, Tephritidae)

Camiel Doorenweerd¹, Luc Leblanc², Allen L. Norrbom³, Michael San Jose¹, Daniel Rubinoff¹

I University of Hawaii, Department of Plant and Environmental Protection Services, 3050 Maile Way, Honolulu, Hawaii, 96822-2231, USA 2 University of Idaho, Department of Entomology, Plant Pathology and Nematology, 875 Perimeter Drive, MS2329, Moscow, Idaho, 83844-2329, USA 3 Systematic Entomology Laboratory, ARS, USDA, c/o Smithsonian Institution, P.O. Box 37012, MRC 168, Washington, DC 20013-7012, USA

Corresponding author: Camiel Doorenweerd (camiel.doorenweerd@hawaii.edu)

Academic editor: <i>M. De Meyer</i> Received 20 October 2017 Accepted 14 December 2017 Pr	ublished 17 January 2018
- http://zoobank.org/F1BF770B-254D-4F8F-976B-A2F53A7E4A60	

Citation: Doorenweerd C, Leblanc L, Norrbom AL, Jose MS, Rubinoff D (2018) A global checklist of the 932 fruit fly species in the tribe Dacini (Diptera, Tephritidae). ZooKeys 730: 19–56. https://doi.org/10.3897/zookeys.730.21786

Abstract

The correct application of the scientific names of species is neither easy nor trivial. Mistakes can lead to the wrong interpretation of research results or, when pest species are involved, inappropriate regulations and limits on trade, and possibly guarantine failures that permit the invasion of new pest species. Names are particularly challenging to manage when groups of organisms encompass a large number of species, when different workers employ different philosophical views, or when species are in a state of taxonomic flux. The fruit fly tribe Dacini is a species-rich taxon within Tephritidae and contains around a fifth of all known species in the family. About 10% of the 932 currently recognized species are pests of commercial fruits and vegetables, precipitating quarantines and trade embargos. Authoritative species lists consist largely of scattered regional treatments and outdated online resources. The checklist presented here is the first global overview of valid species names for the Dacini in almost two decades, and includes new lure records. By publishing this list both in paper and digitally, we aim to provide a resource for those studying fruit flies as well as researchers studying components of their impact on agriculture. The list is largely a consolidation of previous works, but following the results from recent phylogenetic work, we transfer one subgenus and eight species to different genera: members of the Bactrocera subgenus Javadacus Hardy, considered to belong to the Zeugodacus group of subgenera, are transferred to genus Zeugodacus; Bactrocera pseudocucurbitae White, 1999, stat. rev., is transferred back to Bactrocera from Zeugodacus; Zeugodacus arisanicus Shiraki, 1933, stat. rev., is transferred back to Zeugodacus from Bactrocera; and Z.

Copyright Camiel Doorenweerd et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

brevipunctatus (David & Hancock, 2017), comb. n.; Z. javanensis (Perkins, 1938), comb. n.; Z. montanus (Hardy, 1983), comb. n.; Z. papuaensis (Malloch, 1939), comb. n.; Z. scutellarius (Bezzi, 1916), comb. n.; Z. semisurstyli (Drew & Romig, 2013), comb. n.; and Z. trilineatus (Hardy, 1955), comb. n. are transferred from *Bactrocera* to Zeugodacus.

Keywords

global, pest, cryptic, Bactrocera, Zeugodacus, Dacus

Introduction

Despite the current 'phylogenomic' age and the generation of large amounts of data on relatively few, selected, organisms, discovering and classifying new species is an ongoing endeavor of basic science that is far from complete (Zhang 2011). Major challenges to advance taxonomic work lie, among others, in the correct application of scientific species names, which in turn depends on the availability of accurate reference databases. Global initiatives to provide reference lists of species names (e.g., Roskov et al. 2017) all include major gaps that can only be filled by taxonomic specialists. Some groups of organisms are particularly challenging to manage because of the number of species they encompass, conceptual differences between workers, or the existence of unresolved problems with species identities or concepts themselves. Simultaneously, those same groups will likely benefit the most from an authoritative overview.

The fruit fly tribe Dacini is a species-rich radiation within Tephritidae and contains around a fifth of all known species in the family (Norrbom et al. 1999, Pape et al. 2011, Schutze et al. 2017). All Dacini members are frugivorous or florivorous and about 10% of the 932 currently recognized species are pests of commercial fruits and vegetables (Fletcher 1987, White and Elson-Harris 1992, Vargas et al. 2015, Freidberg et al. 2017). Among these are some of the world's economically most important pests, such as the widely introduced oriental fruit fly, Bactrocera dorsalis (Hendel, 1912), carambola fruit fly Bactrocera carambolae Drew & Hancock, 1994, and the melon fly, Zeugodacus cucurbitae (Coquillett, 1899) (De Meyer et al. 2015, Ekesi et al. 2016). The tribe as a whole has received considerable taxonomic attention and new species are continuously being discovered (Fig. 1; Leblanc et al. 2015a, David et al. 2016, 2017). Dacini flies are phenotypically very similar and therefore also one of the most difficult groups of Tephritidae to identify to species-level. Whereas many Tephritidae can be identified from their intricate wing patterns, which are commonly thought to have evolved to deter predators (such as Salticidae jumping spiders [Whitman et al. 1988]), for mating rituals, or territorial behavior, the wings of most Dacini are clear with only a costal band and, usually, an anal streak. The adult chaetotaxy is a set of characters that is usually of value in dipteran species identification, but in Dacini the number of setae is reduced and similar configurations may often be homoplaseous (Hardy 1955, Hancock and Drew 2015). Their body colors, various combinations of black and yellow to red, are commonly thought to have resulted from wasp mimicry and may be under se-



Figure 1. Accumulation of described species in Dacini through time, with publications that featured large numbers of newly described species indicated at their respective moment. The first species was described in 1790, but during the past fifty years the number of recognized [or known] species has more than doubled to reach the current 932.

lective pressure (White 2006). Diagnostic body color patterns used to separate species are further confounded by considerable intraspecific variation (Leblanc et al. 2015b). The combination of these factors has resulted in a long history of unstable classification and even though molecular phylogenetic studies are now reaching a general consensus, this has not fully trickled down to the nomenclatural level.

Dacini is a tropical and subtropical evolutionary radiation of flies with centers of diversity in Southeast Asia and Sub-Saharan Africa. Early molecular phylogenetic studies focused on pest species, often of a particular region, leading to biased results on the relationships between species that may not accurately reflect monophyletic origins or sister-group assignments (Smith et al. 2003, Nakahara and Muraji 2008, Virgilio et al. 2015). With phylogenetic studies expanding their scope beyond the pest species and increased use of molecular data, it became clear that the initial morphology-based classifications had to be revised and, in particular, the large genus *Bactrocera* had to be split into *Bactrocera* and *Zeugodacus* because the latter is more closely related to *Dacus* (Krosch et al. 2012, Virgilio et al. 2015, San Jose et al. 2018 in press, Dupuis et al. 2017). Following the most recent results, there are currently four genera in Dacini: *Monacrostichus* Bezzi, *Dacus* Fabricius, *Bactrocera* Macquart and *Zeugodacus* Hendel

(De Meyer et al. 2015, Virgilio et al. 2015, Freidberg et al. 2017), although some authors (e.g., Drew and Romig 2013, 2016, Hancock and Drew 2016) continue to include Zeugodacus within Bactrocera. Ichneumonopsis Hardy is now placed in Gastrozonini (Norrbom et al. 1999, Freidberg et al. 2017). Aside from shifts in generic assignments, taxa have been variably assigned to species complexes, species groups, subgenera and species-complex groups to provide some additional systematic structure, primarily for the purpose of identification keys (Clarke et al. 2005, White 2006, Drew and Romig 2013). These intermediate taxonomic ranks are mostly groups of convenience defined by unique combinations of characters rather than by synapomorphic characters. The largest and most intesively studied is the Bactrocera dorsalis complex with 88 species; the group that, incidentally, also holds the largest number of pest species. This complex, like most others, is not monophyletic (Leblanc et al. 2015b, Virgilio et al. 2015, San Jose et al. 2018 in press) and there has been synonymy of several significant pest species, such as *B. papayae* Drew & Hancock, 1994, and *B.* invadens Drew, Tsuruta & White, 2005 with B. dorsalis (San Jose et al. 2013, Schutze et al. 2015a, 2015b). To facilitate communication and progress of our understanding of the group, a reliable taxonomic starting point is badly needed and will enable further studies into the taxonomy and systematics of the tribe.

The most recently published catalogs that covered Dacini globally are now almost two decades old (Norrborn et al. 1999, Norrborn 2004) and scattered regional treatments and keys currently comprise the largest body of references for Dacini. For Southeast Asia, there is a relatively recent two-part work including a revision (Drew and Romig 2013) and the accompanying keys that followed (Drew and Romig 2016). These books have incorporated the previous keys for the *B. dorsalis* complex of Drew and Hancock (1994), but they did not adopt the latest results from a series of molecular phylogenetic works, including the split of Bactrocera into Bactrocera and Zeugodacus. For other regions, all treatments are older with increased confusion due to differing morphological terminology, species designations, and assignments. For Africa, the most recent works are two treatments from 2006 (Hancock and Drew 2006, White 2006), and for Australasia there is a treatment from 1989 (Drew 1989), including keys, a proposed subgeneric classification, and revisions for the species in the region. As of 2017, the Drew and Romig books on the Asian fauna are in print and available for sale, and the other works are available digitally online and provide important catalogue references. Online resources that aim to provide up-todate species checklists such as Systema Dipterorum (Pape and Thompson 2013), the Catalogue of Life (Roskov et al. 2017), or the pest-oriented database of the Centre for Agriculture and Biosciences (CABI 2017) are outdated and have not been able to combine the regional treatments appropriately. Valid and invalid names can be verified using the Tephritidae Databases on the COFFHI website (https://coffhi. cphst.org/), but it was primarily designed for host plant information and the tephritid name searches are currently undergoing revision. Other websites, such as the "True Fruit Flies of the Afrotropical Region" (De Meyer and White 2016) or the "PACIFLY" website, covering the Pacific region (Pest Management in the Pacific Project 2003),

contain valuable information, but are limited in scope and are irregularly maintained due to sporadic funding. The checklist presented here is a global overview of valid species names of Dacini. By publishing this list in paper and digital format we hope to provide a resource for those studying fruit fly taxonomy as well as researchers concerned with their impacts on agriculture. The list is largely a consolidation of previous works, but following the results from recent phylogenetic work (Virgilio et al. 2015, San Jose et al. 2018 in press), we transfer one subgenus and eight species to different genera: Bactrocera subgenus Javadacus Hardy, considered to belong to the Zeugodacus group of subgenera by Hancock and Drew (2017), is transferred to genus Zeugodacus; Bactrocera pseudocucurbitae White, 1999, stat. rev., is transferred back to Bactrocera from Zeugodacus; Zeugodacus arisanicus Shiraki, 1933, stat. rev., is transferred back to Zeugodacus from Bactrocera; and Z. brevipunctatus (David & Hancock, 2017a), comb. n., Z. javanensis (Perkins, 1938), comb. n., Z. montanus (Hardy, 1983), comb. n., Z. papuaensis (Malloch, 1939), comb. n., Z. scutellarius (Bezzi, 1916), comb. n., Z. semisurstyli (Drew & Romig, 2013), comb. n., and Z. trilineatus (Hardy, 1955), comb. n. are transferred from Bactrocera to Zeugodacus.

Methods

Checklist

The source data is, for a large part, comprised of regional treatments (Drew 1989, Hancock and Drew 2006, White 2006, Drew and Romig 2013), with additions and revisions from more recent studies (Drew et al. 2011, Yu et al. 2012, Hancock 2015, Hancock and Drew 2015, Hendrichs et al. 2015, Schutze et al. 2015b, David et al. 2016, 2017, Drew and Hancock 2016, Freidberg et al. 2017, Han et al. 2017). Species included in the list are ordered alphabetically by genus. We do not indicate subgeneric or species complex ranks because their biological significance is, at present, unclear (Leblanc et al. 2015b). We do, however, provide the checklist also in spreadsheet form in supplementary material (S1) where these ranks are included and users can sort the species to their preference. For distribution, we use a coarse geographical indication: African or Asia-Pacific. The native region is indicated in the line with the species name, invasive regions are mentioned in the notes. We also include known male lure records for each species: cue-lure, methyl eugenol, isoeugenol and zingerone. Zingerone, first reported as a male lure by Tan and Nishida (2000), has received increased attention in recent years, with new lure records, including species not attracted to the two other lures, for a number of species in Australia and Papua New Guinea (Fay 2012, Royer et al. 2015, 2017). These records are included in the list, along with previously unpublished new records, indicated as such, from our team's recent surveys carried out in Taiwan, Vietnam, Sri Lanka, Bangladesh and Nepal. For morphological terminology we follow White et al. (2000), which follows that in standard usage for other Diptera and differs somewhat from the older treatments.

Conflicting views

For some species that have recently been synonymized or where there are conflicting views by different authors, we have indicated this under the 'notes' for the respective species, so that this may help users to place different views in perspective. It should also be noted that some authors do not follow the elevation of Zeugodacus to genuslevel, because this is currently only supported by molecular data and morphological studies are inconclusive (David et al. 2017, Virgilio et al. 2015, San Jose et al. 2018). This affects the placement of nearly 200 species and although we agree that the reassignment of species may have initially been premature, recent studies corroborate the need to recognize Zeugodacus as a genus to maintain Bactrocera as monophyletic. A 168-species seven-gene phylogeny, including multiple Bactrocera subgenera, shows that Zeugodacus, Bactrocera and Dacus each are monophyletic, and provides moderate statistical support for a sister relationship between Zeugodacus and Dacus (San Jose et al. 2018). A phylogeny with less representatives from Dacini, but 878 molecular loci, provides full statistical support for the sister relationship of Zeugodacus with Dacus, and Bactrocera as sister to both (Dupuis et al. 2017). As such, Bactrocera in the old sense is paraphyletic.

Gender agreement

Because Dacini includes both masculine and feminine genera and because species have been moved between different genera over time, there is some confusion in the literature regarding the correct application of gender agreement. We have paid particular attention to this in the checklist. Most notably, several species names ending in -fer have originally been described without the author indicating if the name should be regarded as a noun or as an adjective. Following section 31.2.2 of the Zoological Code of Zoological Nomenclature (ICZN 1999), such names should be treated as a noun in apposition and the ending should not change when the species is moved to a different genus. This applies to *Bactrocera terminifer* (Walker, 1860), *B. speculifer* (Walker, 1865) and *B. curvifer* (Walker, 1860).

Results

An overview of the current numbers of species split per genus, worldwide and according to the region where they are native, is shown in Table 1. Five species are shared between Africa and the Asia-Pacific regions: *Dacus ciliatus, Bactrocera oleae, B. dorsalis, B. latifrons* and *Zeugodacus cucurbitae*. There are no Dacini native to other regions, however, some species have become invasive in various countries outside their native distribution, such as *B. dorsalis, B. latifrons* and *Z. cucurbitae* from Asia introduced to Africa and various Pacific islands, *B. zonata* introduced from Asia to the Indian Ocean islands and the Middle East, including Egypt, and Asian *B. carambolae*, that invaded

	Worldwide	Africa	Asia-Pacific
Dacini	932	207	730
Bactrocera	461	13	451
Zeugodacus	196	1	195
Dacus	273	193	81
Monacrostichus	2	0	2

Table 1. Number of described species per region.

the Guianas and northern Brazil in South America. Two invasive species are native to Africa; *B. oleae* was introduced to the Mediterranean area, western Asia and California and northwestern Mexico in North America, and *D. ciliatus* has invaded the Middle East and the Indian subcontinent (Vargas et al. 2015).

Checklist

Genus Bactrocera Macquart

Bactrocera abbreviata (Hardy, 1974). Asia-Pacific. Non-pest. Zingerone.

Notes: Zingerone is a new lure record. *Bactrocera abbreviata* may be a junior synonym of *B. bipistulata*. There are morphological intermediates from Sri Lanka in the UHIM collection with a dark facial band and darker femora.

Bactrocera abdofuscata (Drew, 1971). Asia-Pacific. Non-pest.

Bactrocera abdolonginqua (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera abdomininigra Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera abdonigella (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aberrans (Hardy, 1951). Asia-Pacific. Non-pest. Isoeugenol.

Notes: Weakly attracted to isoeugenol (Royer 2015)

Bactrocera abscondita (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera absidata Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera abundans Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aceraglans White & Evenhuis, 1999. Asia-Pacific. Non-pest.

Bactrocera aceromata White & Evenhuis, 1999. Asia-Pacific. Non-pest.

Bactrocera aemula Drew, 1989 Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aenigmatica (Malloch, 1931). Asia-Pacific. Non-pest.

Bactrocera aeroginosa (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure, zingerone.

Bactrocera aethriobasis (Hardy, 1973). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera affinibancroftii Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera affinidorsalis (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera affinis (Hardy, 1954). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera aglaiae (Hardy, 1951). Asia-Pacific. Non-pest. Methyl eugenol, zingerone. *Bactrocera aithogaster* Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera albistrigata de Meijere, 1911. Asia-Pacific. Fruit pest (polyphagous). Cue-lure. Notes: *B. albistrigata* is very similar in appearance to *B. frauenfeldi*. Based on UHIM collection material, the morphological variation of both species is larger than Drew and Romig (2013) suggest. Hardy (1954) considered them synonyms, but they are treated as different species in Drew and Romig (2013). Their populations are likely allopatric, but there appears to be some morphological overlap.

```
Bactrocera allwoodi (Drew, 1979). Asia-Pacific. Non-pest. Cue-lure.
```

Bactrocera amarambalensis Drew, 2002. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera ampla (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera amplexa (Munro, 1984). Africa. Non-pest.

Bactrocera amplexiseta (May, 1962). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera andamanensis (Kapoor, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera anfracta Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera angustifasciata Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera anomala (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera anthracina (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera antigone (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera apicofuscans White & Tsuruta, 2001. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera apiconigroscutella Drew, 2002. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera apicopicta Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aquila (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aquilonis (May, 1965). Asia-Pacific. Fruit pest. Cue-lure.

Notes: May be a junior synonym of *B. tryoni*. The latter is supposedly restricted to the eastern side of Australia, *B. aquilonis* to the west. Even though these populations may now be largely allopatric, separated by the arid regions along the border between the Northern Territories and Queensland, they cannot be separated reliably based on morphology or using a population genetic approach with microsatellite data (Gilchrist et al. 2003, Cameron et al. 2010).

Bactrocera arecae (Hardy & Adachi, 1954). Asia-Pacific. Fruit pest (monophagous).

Bactrocera assita Drew, 1989 Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aterrima (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera atra (Malloch, 1938). Asia-Pacific. Non-pest. Cue-lure.

Notes: Cue-lure is a new lure record from surveys in French Polynesia in 1998. Bactrocera atrabifasciata Drew & Romig, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera atramentata (Hering, 1941). Asia-Pacific. Fruit pest (monophagous). Cuelure, zingerone.

Bactrocera atrifemur Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera atriliniellata* Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aurantiaca (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera aurea (May, 1952). Asia-Pacific. Non-pest. Zingerone.

Bactrocera avittata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. *Bactrocera balagawii* Drew, 2011. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera alyxiae (May, 1953). Asia-Pacific. Non-pest. Cue-lure, zingerone.

Bactrocera bancroftii (Tryon, 1927). Asia-Pacific. Fruit pest (oligophagous). Methyl eugenol. *Bactrocera banneri* White, 1999. Asia-Pacific. Non-pest.

Notes: *B. banneri* and *B. coracina* are the two members of the subgenus *Perkinsidacus* in the most recent treatment of these species (Hancock and Drew 2017b), and both may belong in the genus *Zeugodacus*. They have the shallow emargination of sternite V and the long surstylus lobes of the male genitalia that fit with *Zeugodacus*, but lack a medial vitta on the scutum and the lateral vittae do not extend anteriorly beyond the transverse suture. Because there is, at present, no molecular data to support either placement and because it is unclear which, if any, of these morphological characters are apomorphic we tentatively leave both species in *Bactrocera*.

Bactrocera barringtoniae (Tryon, 1927). Asia-Pacific. Non-pest.

Bactrocera batemani Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera beckerae (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bellisi Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bhutaniae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera biarcuata (Walker, 1865). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera bidentata (May, 1963). Asia-Pacific. Non-pest.

Bactrocera bifasciata (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera biguttula (Bezzi, 1922). Africa. Non-pest.

Bactrocera bimaculata Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. *Bactrocera binhduongiae* Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera bipustulata* (Bezzi, 1914). Asia-Pacific. Non-pest. Cue-lure, zingerone.

Notes: Zingerone is a new lure record. See further comments under *B. abbreviata*. *Bactrocera bitungiae* Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bivittata Lin & Wang, 2005. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera blairiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera brachycera* (Bezzi, 1916). Asia-Pacific. Non-pest.

Bactrocera breviaculeus (Hardy, 1951). Asia-Pacific. Non-pest. Cue-lure, zingerone.

Bactrocera brevistriata (Drew, 1968). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bruneiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera brunnea (Perkins & May, 1949). Asia-Pacific. Non-pest.

Bactrocera brunneola White & Tsuruta, 2001. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bryoniae (Tryon, 1927). Asia-Pacific. Fruit pest (oligophagous). Cue-lure, zingerone.

Bactrocera buinensis Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera bullata Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera bullifera (Hardy, 1973). Asia-Pacific. Non-pest.

Bactrocera buloloensis Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera cacuminata (Hering, 1941). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera caledoniensis Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera caliginosa (Hardy, 1970). Asia-Pacific. Non-pest.

Bactrocera calophylli (Perkins & May, 1949). Asia-Pacific. Non-pest.

Bactrocera captiva Drew & Romig, 2013. Asia-Pacific. Non-pest.

Bactrocera carambolae Drew & Hancock, 1994. Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol, zingerone.

Notes: Under laboratory conditions, B. carambolae and B. dorsalis can produce fertile F1 hybrids, though with reduced survivability, and there is evidence for hybridization in the wild. Nonetheless, based on a combination of genetic and morphological evidence, they are considered to be two separate species (Ebina and Ohto 2006, Schutze et al. 2015a). The native distribution of *B. carambolae* is in Southeast Asia, but it is invasive in South America (Guianas and northern Brazil). Bactrocera carbonaria (Hendel, 1927). Asia-Pacific. Non-pest. Cue-lure. Bactrocera careofascia Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera caryeae (Kapoor, 1971). Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol. Bactrocera ceylanica Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera cheesmanae (Perkins, 1939). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera chettalli David & Ranganath, 2016. Asia-Pacific. Non-pest. Bactrocera cibodasae Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera cinnabaria Drew & Romig, 2013. Asia-Pacific. Non-pest. Bactrocera cinnamea Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera circamusae Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera citima (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure. Bactrocera cogani White, 2006. Africa. Non-pest. Bactrocera cognata (Hardy & Adachi, 1954). Asia-Pacific. Non-pest. Bactrocera collita Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera commensurata Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera commina Drew, 1989. Asia-Pacific. Non-pest. Bactrocera confluens (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera congener Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera consectorata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera contermina Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera contigua Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera continua (Bezzi, 1919). Asia-Pacific. Non-pest. Bactrocera coracina (Drew, 1971). Asia-Pacific. Non-pest. Notes: Maybe should be moved to Zeugodacus, see comments under B. banneri. Bactrocera correcta (Bezzi, 1916). Asia-Pacific. Fruit pest. (polyphagous). Methyl eugenol. Bactrocera costalis (Shiraki, 1933). Asia-Pacific. Non-pest. Cue-lure. Bactrocera curreyi Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera curtivitta Drew & Romig, 2013. Asia-Pacific. Non-pest. Bactrocera curvifer (Walker, 1864). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera curvipennis (Froggatt, 1909). Asia-Pacific. Fruit pest. Cue-lure. Bactrocera curvosterna Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera dapsiles Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera daruensis Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera decumana (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera decurtans (May, 1965). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera diallagma Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera diaphana (Hering, 1953). Asia-Pacific. Non-pest.

- *Bactrocera digressa* Radhakrishnan, 1999. Asia-Pacific. Non-pest. Cue-lure, zingerone. Notes: Zingerone is a new lure record.
- Bactrocera diospyri Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera dispar (Hardy, 1982). Asia-Pacific. Non-pest.

Bactrocera distincta (Malloch, 1931). Asia-Pacific. Fruit pest. Cue-lure.

Bactrocera dongnaiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera dorsalis (Hendel, 1912). Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol, zingerone.

Notes: *B. dorsalis*, the Oriental fruit fly, is one of the most significant pest species within the Tephritidae, and it is invasive in many areas of Asia, Africa and the Pacific islands (Vargas et al. 2015). Based on a total-evidence approach, *B. papayae*, *B. invadens* and *B. philippinensis* are now considered synonyms of *B. dorsalis*, but these names can still be found in numerous papers and internet website resources. *Bactrocera dorsalis* is known to hybridize with *B. carambolae* and genetic evidence suggests that there is historic hybridization with *B. kandiensis* (Schutze et al. 2015b); see notes under those respective species for further details.

Bactrocera dorsaloides (Hardy & Adachi, 1954). Asia-Pacific. Non-pest.

Bactrocera dyscrita (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera ebenea (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera ektoalangiae Drew & Hancock, 1999. Asia-Pacific. Non-pest.

Bactrocera elongata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera endiandrae (Perkins & May, 1949). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera enochra (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera epicharis (Hardy, 1970). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera erubescentis (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera eurycosta Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera exigua (May, 1958). Asia-Pacific. Non-pest.

Bactrocera eximia Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera expandens (Walker, 1859). Asia-Pacific. Fruit pest.

Bactrocera exspoliata (Hering, 1941). Asia-Pacific. Non-pest.

Bactrocera facialis (Coquillett, 1909). Asia-Pacific. Fruit pest. Cue-lure.

Bactrocera fagraea (Tryon, 1927). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera fastigata Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera fergussoniensis Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera fernandoi Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera finitima Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera flavinotus (May, 1957). Asia-Pacific. Non-pest.

Bactrocera flavipennis (Hardy 1982). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera flavoscutellata Lin & Wang, 2005. Asia-Pacific. Non-pest. Cue-lure.

Notes: This is likely a junior synonym of *B. pernigra*. The only distinguishing character is in the width of the basal dark band on the scutellum, but this appears to be

variable (Drew and Romig 2013). Because the characters have only been studied in small sample sizes there has not yet been an official synonymy.

Bactrocera flavosterna Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera floresiae Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera frauenfeldi (Schiner, 1868). Asia-Pacific. Fruit pest (polyphagous). Cue-lure,

zingerone.

Notes: See under B. albistrigata.

Bactrocera froggatti (Bezzi, 1928). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera fuliginus (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure. Bactrocera fulvicauda (Perkins, 1939). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera fulvifacies (Perkins, 1939). Asia-Pacific. Non-pest. Bactrocera fulvifemur Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera fulvosterna Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera furcata David & Hancock, 2017. Asia-Pacific. Non-pest. Bactrocera furfurosa Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera furvescens Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera furvilineata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera fuscalata Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera fuscitibia Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera fuscoformosa Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera fuscohumeralis White & Evenhuis, 1999. Asia-Pacific. Non-pest. Bactrocera fuscolobata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera fuscoptera Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera garciniae Bezzi, 1913. Asia-Pacific. Non-pest. Bactrocera gnetum Drew & Hancock, 1995. Asia-Pacific. Non-pest. Bactrocera gombokensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera grandifasciata White & Evenhuis, 1999. Asia-Pacific. Non-pest. Bactrocera grandistylus Drew & Hancock, 1995. Asia-Pacific. Non-pest. Bactrocera halfordiae (Tryon, 1927). Asia-Pacific. Fruit pest. Bactrocera halmaherae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera hantanae Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera harrietensis Ramani & David, 2016. Asia-Pacific. Non-pest. Bactrocera hastigerina (Hardy, 1954). Asia-Pacific. Fruit pest (monophagous). Bactrocera hispidula (May, 1958). Asia-Pacific. Non-pest. Bactrocera hollingsworthi Drew & Romig, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera holtmanni (Hardy, 1974). Asia-Pacific. Non-pest. Cue-lure. Bactrocera humilis (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Bactrocera hyalina (Shiraki, 1933). Asia-Pacific. Non-pest. Bactrocera hypomelaina Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera icelus (Hardy, 1974). Asia-Pacific. Non-pest. Notes: We continue the use of a masculine epithet like in previous treatments.

Hardy did not give an etymology in his description of the species, but 'icelus' could

refer to the Greek mythical figure by that name, or reference to the Greek word for 'appearance', and we treat it as a noun in aposition.

Bactrocera illusioscutellaris Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure, zingerone.

Notes: Zingerone is a new lure record.

- Bactrocera impunctata (de Mejeire, 1914). Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera incompta Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera inconspicua Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera inconstans Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera indecora (Drew 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera indonesiae Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Zingerone.

Bactrocera infulata Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera invisitata* Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera involuta (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Datrotta mootaa (Tardy, 1902). Asia-racine. Non-pest. Cae-faire.

Bactrocera irvingiae Drew & Hancock, 1994. Asia-Pacific. Non-pest.

Bactrocera ismayi Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Notes: Methyl eugenol is a new lure record from surveys in Papua New Guinea in 1997/1999.

Bactrocera jaceobancroftii Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera jarvisi* (Tryon, 1927). Asia-Pacific. Fruit pest. Cue-lure, zingerone.

Bactrocera kalimantaniae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera kanchanaburi Drew & Hancock ,1994. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera kandiensis Drew & Hancock, 1994. Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol.

Notes: There is likely some (historical) introgression or hybridization between *B. kandiensis* and *B. dorsalis*, and the two cannot be separated reliably using mitochondrial genes (Schutze et al. 2015a, 2015b, San Jose, unpublished data).

Bactrocera kelaena Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera kinabalu Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera kirki (Froggatt, 1910). Asia-Pacific. Fruit pest. Cue-lure.

Bactrocera kohkongiae Leblanc, 2015. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera kraussi (Hardy, 1951). Asia-Pacific. Fruit pest. Cue-lure.

Bactrocera kuniyoshii (Shiraki, 1968). Asia-Pacific. Non-pest.

Bactrocera laithieuiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera lampabilis (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera lata (Perkins 1938). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera lateritaenia Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera laticaudus (Hardy, 1950). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera laticosta Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera latifrons (Hendel, 1915). Asia-Pacific. Fruit pest (oligophagous).

Notes: Native to Asia and introduced into Africa and Hawaii.

Bactrocera latilineata Drew, 1989. Asia-Pacific. Non-pest.

Notes: Male attractant uncertain, previous lure records are likely incorrect (see Drew 1989).

Bactrocera latilineola Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera latissima* Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

- Bactrocera limbifera (Bezzi, 1919). Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera linduensis Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera lineata (Perkins, 1939). Asia-Pacific. Fruit pest (monophagous). Cue-lure.

Bactrocera lombokensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera longicornis Macquart, 1835. Asia-Pacific. Non-pest. Cue-lure.

Notes: Type species for the genus (see Hardy 1976).

Bactrocera lucida (Munro, 1939). Africa. Non-pest.

Bactrocera luteola (Malloch, 1931). Asia-Pacific. Non-pest.

Bactrocera maculigera Doleschall, 1858. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera makilingensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera malaysiensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera mamaliae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera manskii (Perkins & May, 1949). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera matsumurai (Shiraki, 1933). Asia-Pacific. Non-pest.

Bactrocera mayi (Hardy, 1951). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera mcgregori (Bezzi, 1919). Asia-Pacific. Non-pest.

Bactrocera mediorufula Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera megaspilus (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera melania (Hardy & Adachi, 1954). Asia-Pacific. Non-pest.

Bactrocera melanogaster Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera melanoscutata Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera melanothoracica Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera melanotus (Coquillett, 1909). Asia-Pacific. Fruit pest. Cue-lure.

Bactrocera melas (Perkins & May, 1949). Asia-Pacific. Fruit pest. Cue-lure.

Notes: It is uncertain if *B. melas* is a distinct species. Specimens identified as *B. melas* may be a dark form of *B. tryoni*, or hybrids of *B. tryoni* and *B. neohumeralis* (see Hancock et al. 2000).

Bactrocera melastomatos Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera memnonia (Drew, 1989). Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera menanus (Munro, 1984). Africa. Non-pest.

Bactrocera mendosa (May, 1958). Asia-Pacific. Non-pest.

Bactrocera merapiensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera mesomelas (Bezzi, 1908a). Africa. Fruit pest (monophagous).

Bactrocera mesonotaitha Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera mesonotochra Drew, 1989. Asia-Pacific. Non-pest.

Bactrocera mimulus Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera minax (Enderlein, 1920). Asia-Pacific. Fruit pest.

Bactrocera minuscula Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol.

Bactrocera minuta (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.

Bactrocera moluccensis (Perkins, 1939). Asia-Pacific. Fruit pest (monophagous). Cuelure, zingerone.

Bactrocera montyanus (Munro, 1984). Africa. Non-pest. Bactrocera morobiensis Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera morula Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera mucronis (Drew, 1971). Asia-Pacific. Fruit pest. Cue-lure. Bactrocera muiri (Hardy & Adachi, 1954). Asia-Pacific. Non-pest. Bactrocera munroi White, 2004. Africa. Non-pest. Bactrocera murrayi (Perkins, 1939). Asia-Pacific. Fruit pest. Zingerone. Bactrocera musae (Tryon, 1927). Asia-Pacific. Fruit pest (oligophagous). Methyl eugenol. Bactrocera mutabilis (May, 1952). Asia-Pacific. Fruit pest. Bactrocera nanoarcuata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera nationigrotibialis Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera naucleae Drew & Romig, 2001. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera neoarecae Drew, 2002. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera neocheesmanae Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera neocognata Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera neofulvicauda Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera neohumeralis (Hardy, 1951). Asia-Pacific. Fruit pest. Cue-lure, zingerone. Bactrocera neonigrita Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera neonigrotibialis Drew, 2002. Asia-Pacific. Non-pest. Cue-lure. Bactrocera neopagdeni Drew, 1989. Asia-Pacific. Non-pest. Bactrocera neopropingua Drew & Hancock, 1994. Asia-Pacific. Non-pest. Bactrocera neoritsemai Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera neoxanthodes Drew & Romig, 2001. Asia-Pacific. Non-pest. Bactrocera nesiotes (Munro, 1984). Africa. Non-pest. Bactrocera nigella (Drew, 1968). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera nigra (Tryon, 1927). Asia-Pacific. Non-pest. Bactrocera nigrescens (Drew, 1968). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera nigrescentis (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera nigricula (Drew, 1989). Asia-Pacific. Non-pest. Bactrocera nigrifacia Zhang Ji & Chen, 2011. Asia-Pacific. Non-pest. Cue-lure. Bactrocera nigrifemorata Li & Wang, 2011. Asia-Pacific. Non-pest. Bactrocera nigrita (Hardy, 1955). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera nigrivenata (Munro, 1937). Africa. Non-pest. Bactrocera nigrofemoralis White & Tsuruta, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera nigroscutata White & Evenhuis, 1999. Asia-Pacific. Non-pest. Bactrocera nigrotibialis (Perkins, 1938). Asia-Pacific. Fruit pest (oligophagous). Cue-lure. Bactrocera nigrovittata Drew, 1989. Asia-Pacific. Non-pest. Bactrocera notatagena (May, 1953). Asia-Pacific. Non-pest. Bactrocera nothaphoebe Drew & Romig, 2013. Asia-Pacific. Non-pest. Bactrocera obfuscata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

- Bactrocera oblineata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera obliqua (Malloch, 1939). Asia-Pacific. Fruit pest.
- Bactrocera obliquivenosa Drew & Romig, 2001. Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera obscura (Malloch, 1931). Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera obscurata (de Mejeire, 1911). Asia-Pacific. Non-pest.
- Bactrocera obscurivitta Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera obtrullata White & Evenhuis, 1999. Asia-Pacific. Non-pest.
- Bactrocera occipitalis (Bezzi, 1919). Asia-Pacific. Fruit pest. Methyl eugenol.
- Notes: The pest status of this species is uncertain and has possibly been overrated in literature, based on a few obscure rearing records cited in Drew and Hancock (1994).
- Bactrocera ochracea Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.
- *Bactrocera ochroma* Drew & Romig, 2013. Asia-Pacific. Fruit pest (monophagous). Methyl eugenol.
- Bactrocera ochromarginis (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera ochrosiae (Malloch, 1942). Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera ochroventer Drew & Romig, 2013. Asia-Pacific. Non-pest.
 - Notes: Male attractant uncertain. Label data of collected specimens suggests that they have been collected both with cue lure and methyl eugenol, which seems unlikely. Possibly the traps have been contaminated.
- *Bactrocera oleae* (Gmelin, 1790). Africa. Fruit pest (monophagous). Notes: *Bactrocera oleae* is thought to be native to sub-Saharan Africa, and invasive in North Africa, southern Europe, western Asia, and California and northwestern Mexico in North America.
- *Bactrocera opacovitta* Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera opiliae* (Drew & Hardy, 1981). Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera osbeckiae Drew & Hancock, 1994. Asia-Pacific. Non-pest.
- Bactrocera pacificae Drew & Romig, 2001. Asia-Pacific. Non-pest.
- Bactrocera pagdeni (Malloch, 1939). Asia-Pacific. Non-pest.
- Bactrocera pallescentis (Hardy, 1955). Asia-Pacific. Non-pest.
- Bactrocera pallida (Perkins & May, 1949). Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera paraarecae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.
- Bactrocera parabancroftii Drew, 2011. Asia-Pacific. Non-pest. Cue-lure.
- *Bactrocera parabarringtoniae* Drew & Hancock, 1999. Asia-Pacific. Non-pest. Cue-lure. *Bactrocera paradiospyri* Chen Zhou & Li, 2011. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera parafrauenfeldi* Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.
- *Bactrocera parafroggatti* Drew & Romig, 2001. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera paralatissima* Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera paralimbifera Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera paramusae Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.
- *Bactrocera paranigrita* Drew & Romi, g 2013. Asia-Pacific. Non-pest. Methyl eugenol. *Bactrocera paraosbeckiae* Drew, 2002. Asia-Pacific. Non-pest. Cue-lure.
- Bactrocera paraverbascifoliae Drew, 2002. Asia-Pacific. Non-pest. Methyl eugenol.
- *Bactrocera paraxanthodes* Drew & Hancock, 1995. Asia-Pacific. Non-pest. Methyl eugenol. Notes: The attraction to methyl eugenol possibly is weak.

Bactrocera parvula (Hendel, 1912). Asia-Pacific. Non-pest. Bactrocera passiflorae (Froggatt, 1910). Asia-Pacific. Fruit pest. Cue-lure. Bactrocera patula Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera pectoralis (Walker, 1859). Asia-Pacific. Non-pest. Bactrocera pedestris (Bezzi, 1913). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pendleburyi (Perkins, 1938). Asia-Pacific. Non-pest. Zingerone. Notes: Zingerone is a new lure record. Bactrocera peneallwoodi Drew & Romig, 2013. Asia-Pacific. Non-pest. Notes: Male attractant uncertain. Label data of collected specimens suggests that they have been collected both with cue lure and methyl eugenol, which seems unlikely. Possibly the traps have been contaminated. Bactrocera penebeckerae Drew & Romig, 2013. Asia-Pacific. Non-pest. Bactrocera penecognata Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera penecorrecta Drew, 2002. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera penecostalis Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera penefurva Drew, 1989. Asia-Pacific. Non-pest. Bactrocera peneobscura Drew & Romig, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera penephaea Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera peninsularis (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pepisalae (Froggatt, 1910). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera perfusca (Aubertin, 1929). Asia-Pacific. Fruit pest. Bactrocera perigrapha White & Tsuruta, 2001. Asia-Pacific. Non-pest. Cue-lure, zingerone. Notes: Zingerone is a new lure record. Bactrocera perkinsi (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pernigra Ito, 1983. Asia-Pacific. Non-pest. Cue-lure. Notes: see comments under B. flavoscutellata Bactrocera peterseni (Hardy, 1970). Asia-Pacific. Non-pest. Bactrocera petila Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera phaea (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera phaleriae (May, 1956). Asia-Pacific. Non-pest. Bactrocera picea (Drew, 1972). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera pictipennis Lin & Zeng, 2011. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera pisinna Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera popondettiensis Drew, 1989. Asia-Pacific. Non-pest. Bactrocera profunda Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera prolixa Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera propedistincta Drew, 1989. Asia-Pacific. Non-pest. Bactrocera propingua (Hardy & Adachi, 1954). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pruniae Drew & Romig, 2013. Asia-Pacific. Fruit pest (monophagous). Bactrocera pseudobeckerae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera pseudocucurbitae White, 1999, stat. rev. Asia-Pacific. Non-pest. Cue-lure. Notes: This species was assigned to the subgenus Parasinodacus by Drew and Romig (2013), and subsequently assigned to genus Zeugodacus by De Meyer et al. (2015). It was assigned to Parasinodacus based on having a medial yellow scutal vitta and having just two scutellar setae, but it differs from other members of *Parasinodacus* in lacking yellow marks anterior to the transverse suture (= notopleural suture of Drew and Romig 2013), the presence of which is likely a reliable character for assignment to *Zeugodacus* (White 1999, San Jose et al. 2018). In a phylogeny based on molecular data from seven genes, the species is reliably placed within the *Bactrocera* clade (San Jose et al. 2018). We therefore here move the species back to *Bactrocera* and tentatively assign it to the subgenus *Bactrocera*.

Bactrocera pseudodistincta (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pseudoversicolor Drew, 2002. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera psidii (Froggatt, 1899). Asia-Pacific. Fruit pest. Cue-lure. Bactrocera pulchra Tryon, 1927. Asia-Pacific. Non-pest. Bactrocera pusilla (Hardy, 1983). Asia-Pacific. Non-pest. Cue-lure. Bactrocera pyrifoliae Drew & Hancock, 1994. Asia-Pacific. Fruit pest (oligophagous). Bactrocera quadrata (May, 1963). Asia-Pacific. Non-pest. Cue-lure. Bactrocera quadrisetosa (Bezzi, 1928). Asia-Pacific. Fruit pest. Bactrocera quasiinfulata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera quasineonigrita Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera quasipropingua Drew & Hancock, 1994. Asia-Pacific. Non-pest. Bactrocera quasisilvicola Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera raiensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera ramuensis Drew, 2011. Asia-Pacific. Non-pest. Cue-lure. Bactrocera ranganathi Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera reclinata Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera recurrens (Hering, 1941). Asia-Pacific. Non-pest. Cue-lure. Bactrocera redunca (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera repanda Drew, 1989. Asia-Pacific. Non-pest. Bactrocera resima (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera retrorsa Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera rhabdota Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera ritsemai (Weyenbergh, 1869). Asia-Pacific. Non-pest. Cue-lure. Bactrocera robertsi Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera robiginosa (May, 1958). Asia-Pacific. Non-pest. Bactrocera romigae (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera rubigina (Wang & Zhao, 1989). Asia-Pacific. Non-pest. Cue-lure, zingerone. Notes: Zingerone is a new lure record. Bactrocera rufescens (May, 1967). Asia-Pacific. Non-pest. Cue-lure. Bactrocera rufivitta Drew, 2011. Asia-Pacific. Non-pest. Cue-lure. Bactrocera rufofuscula (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure, zingerone. Bactrocera russeola (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure. Bactrocera rutengiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol.

- Bactrocera rutila (Hering, 1941). Asia-Pacific. Non-pest.
- Bactrocera samoae Drew, 1989. Asia-Pacific. Non-pest.
Bactrocera sapaensis Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera satanellus (Hering, 1941). Asia-Pacific. Non-pest. Bactrocera seguyi (Hering, 1939). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera selenophora Tsuruta & White, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera sembaliensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera setinervis (Malloch, 1938). Asia-Pacific. Non-pest. Bactrocera silvicola (May, 1962). Asia-Pacific. Non-pest. Cue-lure, zingerone. Bactrocera simulata (Malloch, 1939). Asia-Pacific. Non-pest. Cue-lure. Bactrocera speculifer (Walker, 1865). Asia-Pacific. Fruit pest (monophagous). Methyl eugenol. Bactrocera speewahensis Fay & Hancock, 2006. Asia-Pacific. Non-pest. Zingerone. Bactrocera splendida (Perkins, 1938). Asia-Pacific. Non-pest. Bactrocera strigata (Perkins, 1934). Asia-Pacific. Non-pest. Bactrocera sulawesiae Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera suliae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera sumbawaensis Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera superba Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera symplocos Drew & Romig, 2013. Asia-Pacific. Non-pest. Bactrocera syzygii White & Tsuruta, 2001. Asia-Pacific. Non-pest. Zingerone. Notes: Zingerone is a new lure record. Bactrocera tapahensis Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera tenuifascia (May, 1965). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera terminaliae Drew, 1989. Asia-Pacific. Non-pest. Bactrocera terminifer (Walker, 1860). Asia-Pacific. Non-pest. Bactrocera ternatiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera tetrachaeta (Bezzi, 1919). Asia-Pacific. Non-pest. Bactrocera thailandica Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera thistletoni Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera tigrina (May, 1953). Asia-Pacific. Non-pest. Zingerone. Bactrocera tillyardi (Perkins, 1938). Asia-Pacific. Non-pest. Bactrocera tinomiscii Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera torresiae Huxam & Hancock, 2006. Asia-Pacific. Non-pest. Cue-lure. Bactrocera tortuosa White & Evenhuis, 1999. Asia-Pacific. Non-pest. Bactrocera toxopeusi (Hering, 1953). Asia-Pacific. Non-pest. Bactrocera trifaria (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera trifasciata (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure. Bactrocera trilineola Drew, 1989. Asia-Pacific. Fruit pest. Cue-lure. Bactrocera trivialis (Drew, 1971). Asia-Pacific. Fruit pest. Cue-lure, zingerone. Bactrocera truncata Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Bactrocera tryoni (Froggatt, 1897). Asia-Pacific. Fruit pest. Cue-lure, zingerone. Notes: See under *B. aquilonis*. Bactrocera tsuneonis (Miyake, 1919). Asia-Pacific. Fruit pest. Bactrocera tuberculata (Bezzi, 1916). Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol. Bactrocera turneri Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Bactrocera umbrosa (Fabricius, 1805). Asia-Pacific. Fruit pest (monophagous). Methyl eugenol. Bactrocera unifasciata (Malloch, 1939). Asia-Pacific. Non-pest. Cue-lure. Bactrocera unilineata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera unimacula Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera unipunctata (Malloch, 1939). Asia-Pacific. Non-pest. Bactrocera unistriata (Drew, 1971). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera unitaeniola Drew & Romig, 2001. Asia-Pacific. Non-pest. Cue-lure. Bactrocera usitata Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera ustulata Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Bactrocera uvariae Drew, 2011. Asia-Pacific. Non-pest. Cue-lure. Bactrocera venefica (Hering, 1938). Asia-Pacific. Non-pest. Bactrocera verbascifoliae Drew & Hancock, 1994. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera versicolor (Bezzi, 1916). Asia-Pacific. Fruit pest (monophagous). Methyl eugenol. Bactrocera visenda (Hardy, 1951). Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera vishnu Drew & Hancock, 1994. Asia-Pacific. Non-pest. Cue-lure. Bactrocera vulgaris (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure. Bactrocera waaiae Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera wanangiae Drew & Hancock, 2016. Asia-Pacific. Non-pest. Bactrocera warisensis White & Evenhuis, 1999. Asia-Pacific. Non-pest. Bactrocera wuzhishana Li & Wang, 2006. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera xanthodes (Broun, 1904). Asia-Pacific. Fruit pest. Methyl eugenol. Bactrocera yayeyamana (Matsumara, 1916). Asia-Pacific. Non-pest. Bactrocera yorkensis Drew & Hancock, 1999. Asia-Pacific. Non-pest. Methyl eugenol. Bactrocera zonata (Saunders, 1842). Asia-Pacific. Fruit pest (polyphagous). Methyl eugenol. Notes: Natively distributed in Asia, from the Indian subcontinent to Vietnam, and invasive in the Afrotropical and West-Palearctic (Middle East) Regions. Genus Dacus Fabricius Dacus abbabae Munro, 1933. Africa. Non-pest. Dacus abditus (Munro, 1984). Africa. Non-pest.

Dacus abruptus White, 2009. Africa. Non-pest.

Dacus absonifacies (May, 1956). Asia-Pacific. Non-pest. Cue-lure, zingerone.

Dacus acutus White, 2009. Africa. Non-pest.

Dacus adenae (Hering, 1940). Africa. Non-pest.

Dacus adenionis Munro, 1984. Africa. Non-pest.

Dacus adustus Munro, 1948. Africa. Non-pest.

Dacus aequalis Coquillett, 1909. Asia-Pacific. Non-pest. Cue-lure, zingerone.

Dacus africanus Adams, 1905. Africa. Non-pest. Cue-lure.

Dacus alarifumidus Drew, 1989. Asia-Pacific. Non-pest. Cue-lure.

Dacus albiseta White, 2009. Africa. Non-pest. Cue-lure.

Dacus alulapictus Drew, 1989. Asia-Pacific. Non-pest.

Dacus amberiens (Munro, 1984). Africa. Non-pest.

Dacus ambonensis Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure.

Dacus amphoratus (Munro, 1984). Africa. Non-pest. Dacus aneuvittatus (Drew, 1971). Asia-Pacific. Non-pest. Dacus annulatus Becker, 1903. Africa. Non-pest. Dacus apectus White, 2006. Africa. Non-pest. Dacus apiculatus White, 2006. Africa. Non-pest. Cue-lure. Dacus apostata (Hering, 1937). Africa. Non-pest. Dacus apoxanthus Bezzi, 1924. Africa. Non-pest. Dacus arabicus White, 2006. Africa. Non-pest. Dacus arcuatus Munro, 1939. Africa. Non-pest. Dacus armatus Fabricius, 1805. Africa. Non-pest. Cue-lure. Notes: Type species for the genus. Dacus aspilus Bezzi, 1924. Africa. Non-pest. Dacus atrimarginatus Drew & Hancock, 1998. Asia-Pacific. Non-pest. Dacus attenuatus Collart, 1935. Africa. Non-pest. Dacus axanthinus White & Evenhuis, 1999. Asia-Pacific. Non-pest. Dacus axanus (Hering 1938). Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure, zingerone. Notes: Dacus axanus is a species that is common in Australia and Papua New Guinea, and this name appears in various pest-related resources. D. unicolor and D. vespiformis may be conspecific with D. axanus. The latter two were described in a single publication by Hendel (Hendel 1927) without illustrations and the descriptions do not differentiate either from *D. axanus*. The types of *D. unicolor* and *D. vespiformis* were lost during the fire at the Museum in Hamburg in 1943. Dacus badius Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Dacus bakingiliensis Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus bannatus Wang, 1990. Asia-Pacific. Non-pest. Cue-lure. Dacus basifasciatus (Hering, 1941). Africa. Non-pest. Dacus bellulus Drew & Hancock, 1981. Asia-Pacific. Non-pest. Cue-lure, zingerone. Dacus bequaerti Collart, 1935. Africa. Non-pest. Dacus bidens (Curran, 1927). Africa. Non-pest. Dacus binotatus Loew, 1862. Africa. Non-pest. Cue-lure. Dacus bispinosus (Wang, 1990). Asia-Pacific. Non-pest. Dacus bistrigulatus Bezzi, 1908. Africa. Non-pest. Dacus bivittatus (Bigot, 1858). Africa. Cucurbitaceae fruit pest. Cue-lure. Dacus blepharogaster Bezzi, 1917. Africa. Non-pest. Dacus bombastus Hering, 1941. Africa. Non-pest. Dacus botianus (Munro, 1984). Africa. Non-pest. Dacus brevis Coquillett, 1901. Africa. Non-pest. Dacus brevistriga Walker, 1861. Africa. Non-pest. Dacus briani White, 2006. Africa. Non-pest. Dacus brunnalis White, 2009. Africa. Non-pest. Dacus calirayae Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus capillaris (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure. Dacus carnesi (Munro, 1984). Africa. Non-pest.

Dacus carvalhoi (Munro, 1984). Africa. Non-pest. Dacus ceropegiae (Munro, 1984). Africa. Non-pest. Dacus chamun (Munro, 1984). Africa. Non-pest. Dacus chapini Curran, 1927. Africa. Non-pest. Dacus chiwira Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus chrysomphalus (Bezzi, 1924). Africa. Non-pest. Cue-lure. Dacus ciliatus Loew, 1862 Africa. Cucurbitaceae fruit pest. Notes: Native to the Aftrotropical Region, and invasive in the Middle East and the Indian subcontinent (India, Pakistan, Bangladesh, Sri Lanka). Dacus clinophlebs Hendel, 1928. Africa. Non-pest. Dacus coenensis Royer & Hancock, 2012. Asia-Pacific. Non-pest. Cue-lure. Dacus collarti Munro, 1938. Africa. Non-pest. Dacus congoensis White, 2006. Africa. Non-pest. Dacus conopsoides de Meijere, 1911. Asia-Pacific. Non-pest. Dacus copelandi White, 2006. Africa. Non-pest. Dacus crabroniformis (Bezzi, 1914). Asia-Pacific. Non-pest. Dacus croceus Munro, 1957. Africa. Non-pest. Dacus cyathus (Munro, 1984). Africa. Non-pest. Dacus delicatus Munro, 1939. Africa. Non-pest. Dacus deltatus White, 2006. Africa. Non-pest. Dacus demmerezi (Bezzi, 1917). Africa. Cucurbitaceae fruit pest. Cue-lure. Dacus devure Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus diastatus Munro, 1984. Africa. Non-pest. Cue-lure. Dacus discipennis (Walker, 1861). Asia-Pacific. Non-pest. Dacus discophorus (Hering, 1956). Asia-Pacific. Non-pest. Cue-lure. Dacus discors Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Dacus discretus Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Dacus disjunctus (Bezzi, 1915). Africa. Non-pest. Dacus dissimilis Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Dacus donggaliae Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Dacus dorjii Drew & Romig, 2007. Asia-Pacific. Non-pest. Cue-lure. Dacus durbanensis Munro, 1935. Africa. Non-pest. Cue-lure, zingerone. Notes: The attraction to zingerone was documented by Manrakhan et al. (2017). Dacus eclipsis (Bezzi, 1924). Africa. Non-pest. Cue-lure. Dacus elatus White, 2006. Africa. Non-pest. Dacus elegans (Munro, 1984). Africa. Non-pest. Dacus elutissimus Bezzi, 1924. Africa. Non-pest. Dacus eminus Munro 1939. Africa. Non-pest. Cue-lure. Dacus erythraeus Bezzi, 1917. Africa. Non-pest. Dacus esakii (Shiraki, 1939). Asia-Pacific. Non-pest. Dacus etiennellus Munro, 1984. Africa. Non-pest. Cue-lure. Dacus externellus (Munro, 1984). Africa. Non-pest. Dacus famona Hancock, 1985. Africa. Non-pest. Cue-lure.

Dacus fasciolatus Collart, 1940. Africa. Non-pest. Dacus feijeni White, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus ficicola Bezzi, 1915. Africa. Non-pest. Dacus fissuratus White, 2006. Africa. Non-pest. Dacus flavicrus Graham, 1910. Africa. Non-pest. Dacus fletcheri Drew & Romig, 2007. Asia-Pacific. Non-pest. Cue-lure. Dacus formosanus (Tseng & Chu, 1983). Asia-Pacific. Non-pest. Cue-lure. Dacus freidbergi (Munro, 1984). Africa. Non-pest. Dacus frontalis Becker, 1922. Africa. Cucurbitaceae fruit pest. Cue-lure, zingerone. Notes: The attraction to zingerone was documented by Manrakhan et al. (2017). Dacus fumosus Collart, 1935. Africa. Non-pest. Dacus fuscatus Wiedemann, 1819. Africa. Non-pest. Dacus fuscinervis Malloch, 1932. Africa. Non-pest. Dacus fuscovittatus Graham, 1910. Africa. Non-pest. Cue-lure. Dacus gabonensis White, 2006. Africa. Non-pest. Dacus ghesquierei Collart, 1935. Africa. Non-pest. Dacus goergeni De Meyer, White & Goodger, 2013. Africa. Non-pest. Dacus guineensis Hering, 1944. Africa. Non-pest. Dacus gypsoides Munro, 1933. Africa. Non-pest. Dacus hainanus Wang & Zhao, 1989. Asia-Pacific. Non-pest. Dacus hamatus Bezzi, 1917. Africa. Non-pest. Dacus hapalus (Munro, 1984). Africa. Non-pest. Dacus hardyi Drew, 1979. Asia-Pacific. Non-pest. Cue-lure. Dacus hargreavesi (Munro, 1939). Africa. Non-pest. Dacus herensis (Munro, 1984). Africa. Non-pest. Dacus humeralis (Bezzi, 1915). Africa. Non-pest. Cue-lure. Dacus hyalobasis Bezzi, 1924. Africa. Non-pest. Dacus iaspideus Munro, 1948. Africa. Non-pest. Dacus icariiformis (Enderlein, 1920). Asia-Pacific. Non-pest. Dacus ikelenge Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus impar Drew, 1989. Asia-Pacific. Non-pest. Dacus inclytus (Munro, 1984). Africa. Non-pest. Dacus indecorus (Hardy, 1974). Asia-Pacific. Non-pest. Dacus infernus (Hardy, 1973). Asia-Pacific. Non-pest. Dacus inflatus Munro, 1939. Africa. Non-pest. Dacus inornatus Bezzi, 1908. Africa. Non-pest. Dacus insolitus White, 2009. Africa. Non-pest. Dacus insulosus Drew & Hancock, 1998. Asia-Pacific. Non-pest. Dacus jubatus (Munro, 1984). Africa. Non-pest. Dacus kakamega White, 2006. Africa. Non-pest. Dacus kaplanae White, 2009. Africa. Non-pest. Dacus kariba Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus katonae Bezzi, 1924. Africa. Non-pest.

Dacus keiseri (Hering, 1956). Asia-Pacific. Non-pest. Dacus kurrensis White, 2009. Africa. Non-pest. Dacus lagunae Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus langi Curran, 1927. Africa. Non-pest. Cue-lure. Dacus leongi Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus limbipennis Macquart, 1843. Africa. Cucurbitaceae fruit pest. Dacus linearis Collart, 1935. Africa. Non-pest. Dacus longicornis (Wiedemann, 1830). Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure. Dacus longistylus Wiedemann, 1830. Africa. Non-pest. Dacus lotus (Bezzi, 1924). Africa. Non-pest. Dacus lounsburyii Coquillett, 1901. Africa. Cucurbitaceae fruit pest. Dacus luteovittatus White, 2009. Africa. Non-pest. Dacus macer Bezzi, 1919. Africa. Non-pest. Dacus maculipterus Drew & Hancock, 1998. Asia-Pacific. Non-pest. Dacus madagascarensis White, 2006. Africa. Non-pest. Cue-lure. Dacus magnificus White, 2009. Africa. Non-pest. Dacus maprikensis Drew, 1989. Asia-Pacific. Non-pest. Dacus marshalli Bezzi, 1924. Africa. Non-pest. Dacus masaicus Munro, 1937. Africa. Non-pest. Cue-lure. Dacus mayi (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure. Dacus maynei Bezzi, 1924. Africa. Non-pest. Dacus mediovittatus White, 2006. Africa. Non-pest. Cue-lure. Dacus meladassus (Munro, 1984). Africa. Non-pest. Dacus melanaspis (Munro, 1984). Africa. Non-pest. Dacus melanohumeralis Drew, 1989. Asia-Pacific. Non-pest. Methyl eugenol. Dacus melanopectus Drew & Romig, 2013. Asia-Pacific. Non-pest. Methyl eugenol. Dacus merzi White, 2006. Africa. Non-pest. Dacus mirificus (Munro, 1984). Africa. Non-pest. Dacus mochii Bezzi, 1917. Africa. Non-pest. Dacus mulgens Munro, 1932. Africa. Non-pest. Dacus murphyi Drew & Hancock, 1998. Asia-Pacific. Non-pest. Dacus nairobensis White, 2006. Africa. Non-pest. Dacus namibiensis Hancock & Drew, 2001. Africa. Non-pest. Dacus nanggalae Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus nanus Collart, 1940. Africa. Non-pest. Dacus newmani (Perkins, 1937). Asia-Pacific. Non-pest. Cue-lure. Dacus nigriscutatus White, 2006. Africa. Non-pest. Dacus nigrolateris White, 2006. Africa. Non-pest. Dacus notalaxus Munro, 1984. Africa. Non-pest. Dacus nummularius (Bezzi, 1916). Asia-Pacific. Non-pest. Cue-lure. Dacus obesus Munro, 1948. Africa. Non-pest. Dacus okumuae White, 2006. Africa. Non-pest. Dacus ooii Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure.

Dacus opacatus Munro, 1948. Africa. Non-pest. Dacus ortholomatus Hardy, 1982. Asia-Pacific. Non-pest. Dacus ostiofaciens Munro, 1932. Africa. Non-pest. Dacus pallidilatus Munro, 1948. Africa. Non-pest. Cue-lure. Dacus palmerensis Drew, 1989. Asia-Pacific. Non-pest. Cue-lure. Dacus pamelae (Munro, 1984). Africa. Non-pest. Dacus panpyrrhus (Munro, 1984). Africa. Non-pest. Dacus parvimaculatus White, 2006. Africa. Non-pest. Dacus pecropsis Munro, 1984. Africa. Non-pest. Cue-lure. Dacus pedunculatus (Bezzi, 1919). Asia-Pacific. Non-pest. Dacus pergulariae Munro, 1938. Africa. Non-pest. Dacus persicus Hendel, 1927. Asia-Pacific. Non-pest. Dacus petioliforma (May, 1956). Asia-Pacific. Non-pest. Cue-lure. Dacus phantoma Hering, 1941. Africa. Non-pest. Dacus phimis (Munro, 1984). Africa. Non-pest. Dacus phloginus (Munro, 1984). Africa. Non-pest. Dacus pictus (Hardy, 1970). Asia-Pacific. Non-pest. Dacus plagiatus Collart, 1935. Africa. Non-pest. Dacus pleuralis Collart, 1935. Africa. Non-pest. Cue-lure. Dacus polistiformis (Senior-White, 1922). Asia-Pacific. Non-pest. Dacus pseudapostata White, 2009. Africa. Non-pest. Dacus pseudomirificus White, 2009. Africa. Non-pest. Dacus pulchralis White, 2006. Africa. Non-pest. Cue-lure. Dacus pullescens Munro, 1948. Africa. Non-pest. Dacus pullus (Hardy, 1982). Asia-Pacific. Non-pest. Dacus punctatifrons Karsch, 1887. Africa. Cucurbitaceae fruit pest. Cue-lure. Dacus purpurifrons Bezzi, 1924. Africa. Non-pest. Dacus purus (Curran, 1927). Africa. Non-pest. Dacus pusillator (Munro, 1984). Africa. Non-pest. Dacus pusillus (May, 1965). Asia-Pacific. Non-pest. Methyl eugenol. Dacus quilicii White, 2006. Africa. Non-pest. Cue-lure. Dacus radmirus Hering, 1941. Africa. Non-pest. Dacus ramanii Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus rubicundus Bezzi, 1924. Africa. Non-pest. Dacus rufoscutellatus (Hering, 1937). Africa. Non-pest. Dacus rufus Bezzi, 1915. Africa. Non-pest. Dacus rugatus Munro, 1984. Africa. Non-pest. Dacus ruslan (Hering, 1941). Africa. Non-pest. Dacus rutilus Munro, 1948. Africa. Non-pest. Dacus sakeji Hancock, 1985. Africa. Non-pest. Cue-lure. Dacus salamander (Drew & Hancock, 1981). Asia-Pacific. Non-pest. Cue-lure. Dacus santongae Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus satanas (Hering, 1939). Asia-Pacific. Non-pest. Zingerone.

Notes: Zingerone is a new lure record. Dacus scaber Loew, 1862. Africa. Non-pest. Dacus schoutedeni Collart, 1935. Africa. Non-pest. Dacus secamoneae Drew, 1989. Asia-Pacific. Non-pest. Cue-lure, zingerone. Dacus segunii White, 2006. Africa. Non-pest. Cue-lure. Dacus seguyi (Munro, 1984). Africa. Non-pest. Dacus semisphaereus Becker, 1903. Africa. Non-pest. Dacus senegalensis White, 2009. Africa. Non-pest. Dacus serratus (Munro, 1984). Africa. Non-pest. Dacus setilatens Munro, 1984. Africa. Non-pest. Dacus siamensis Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure. Dacus signatifrons (May, 1956). Asia-Pacific. Non-pest. Cue-lure. Dacus siliqualactis Munro, 1939. Africa. Non-pest. Dacus sinensis Wang, 1990. Asia-Pacific. Non-pest. Dacus solomonensis Malloch, 1939. Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure. Dacus sphaeristicus Speiser, 1910. Africa. Non-pest. Dacus sphaeroidalis (Bezzi, 1916). Asia-Pacific. Non-pest. Cue-lure. Dacus sphaerostigma (Bezzi, 1924). Africa. Non-pest. Dacus spissus Munro, 1984. Africa. Non-pest. Dacus stentor Munro, 1929. Africa. Non-pest. Dacus stylifer (Bezzi, 1919). Africa. Non-pest. Dacus subsessilis (Bezzi, 1919). Asia-Pacific. Non-pest. Dacus succaelestis Ito, 2011. Asia-Pacific. Non-pest. Dacus taui Drew & Romig, 2001. Asia-Pacific. Non-pest. Cue-lure. Dacus telfaireae (Bezzi, 1924). Africa. Non-pest. Cue-lure. Dacus temnopterus Bezzi, 1928. Africa. Non-pest. Dacus tenebricus Munro, 1938. Africa. Non-pest. Dacus tenebrosus Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure, zingerone. Notes: Zingerone is a new lure record. Dacus theophrastus Hering, 1941. Africa. Non-pest. Cue-lure. Dacus transitorius Collart, 1935. Africa. Non-pest. Dacus transversalis White, 2009. Africa. Non-pest. Dacus triater Munro, 1937. Africa. Non-pest. Dacus trigonus Bezzi, 1919. Africa. Non-pest. Dacus trimacula Wang, 1990. Asia-Pacific. Non-pest. Cue-lure, zingerone. Notes: Zingerone is a new lure record. Dacus triquetrus Drew & Romig, 2013. Asia-Pacific. Non-pest. Cue-lure. Dacus umbeluzinus (Munro, 1984). Africa. Non-pest. Dacus umbrilatus Munro, 1938. Africa. Non-pest. Dacus umehi White, 2006. Africa. Non-pest. Dacus unicolor (Hendel, 1927). Asia-Pacific. Non-pest.

Dacus velutifrons White, 2009. Africa. Non-pest.

Notes: See under D. axanus

- Dacus venetatus Munro, 1939. Africa. Non-pest. Cue-lure.
- Dacus vertebratus Bezzi, 1908. Africa. Cucurbitaceae fruit pest. Cue-lure.
- Dacus vespiformis (Hendel, 1927). Asia-Pacific. Non-pest.
 - Notes: See under D. axanus.
- Dacus vestigivittatus White, 2009. Africa. Non-pest.
- Dacus viator Munro, 1939. Africa. Non-pest.
- Dacus vijaysegarani Drew & Hancock, 1998. Asia-Pacific. Non-pest. Cue-lure, zingerone.
 - Notes: Zingerone is a new lure record.
- Dacus vittatus (Hardy, 1974). Asia-Pacific. Non-pest.
- Dacus wallacei White, 1998. Asia-Pacific. Non-pest.
- Dacus woodi Bezzi, 1917. Africa. Non-pest.
- Dacus xanthaspis (Munro, 1984). Africa. Non-pest.
- Dacus xanthinus White, 2009. Africa. Non-pest.
- Dacus xanthopterus (Bezzi, 1915). Africa. Non-pest. Cue-lure.
- Dacus xanthopus Bezzi, 1924. Africa. Non-pest.
- Dacus yangambinus Munro, 1984. Africa. Non-pest.
- Dacus yaromi White, 2009. Africa. Non-pest.
- Dacus yemenensis White, 2006. Africa. Non-pest.

Genus Monacrostichus Bezzi

- Monacrostichus citricola (Bezzi, 1913). Asia-Pacific. Fruit pest.
 - Notes: Type species for the genus.
- Monacrostichus malaysiae Drew & Hancock, 1994. Asia-Pacific. Non-pest.

Genus Zeugodacus Hendel

- Zeugodacus abdoangustus (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus abdoaurantiacus (Drew, 1989). Asia-Pacific. Non-pest.
- Zeugodacus abdopallescens (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus ablepharus (Bezzi, 1919). Asia-Pacific. Non-pest.
- Zeugodacus abnormis (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus absolutus (Walker, 1861). Asia-Pacific. Non-pest.
- Zeugodacus aithonota (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus alampetus (Drew, 1989). Asia-Pacific. Non-pest. Methyl eugenol.
- Zeugodacus ambiguus (Shiraki, 1933). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus amoenus (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus anala (Chen & Zhou, 2013). Asia-Pacific. Non-pest.
 - Notes: We regard this name as a noun, not changing the ending, following De Meyer et al. (2015). Chen and Zhou (2013) did not specify if it was meant as a noun or adjective, but mentioned "the specific ephithet refers to the wing anal streak".
- Zeugodacus anchitrichotus (Drew, 1989). Asia-Pacific. Non-pest.
- Zeugodacus angusticostatus (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus angustifinis (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus apicalis (de Meijere, 1911). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus apiciflavus (Yu He & Chen, 2011). Asia-Pacific. Non-pest.

Zeugodacus apicofemoralis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure. Zeugodacus areolatus (Walker, 1861). Asia-Pacific. Non-pest.

Zeugodacus arisanicus Shiraki, 1933, stat. rev. Asia-Pacific. Non-pest. Cue-lure.

Notes: This species is here reassigned to *Zeugodacus*. It has a medial postsutural vitta and yellow markings anterior of the transverse suture, which are likely reliable morphological characters for assignment to *Zeugodacus*. This generic assignment is further supported by DNA sequence data from seven genes (San Jose et al. 2018). Whether the other members assigned to the subgenus *Hemizeugodacus* should be placed in *Bactrocera* or *Zeugodacus* remains to be determined.

Zeugodacus armillatus (Hering, 1938). Asia-Pacific. Non-pest.

Zeugodacus assamensis White, 1999. Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus atrichus (Bezzi, 1919). Asia-Pacific. Non-pest.

Zeugodacus atrifacies (Perkins, 1938). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus atrisetosus (Perkins, 1939). Asia-Pacific. Cucurbitaceae fruit pest.

Zeugodacus atypicus (White & Evenhuis, 1999). Asia-Pacific. Non-pest.

Zeugodacus aurantiventer (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus bakeri (Bezzi, 1919). Asia-Pacific. Non-pest.

Zeugodacus baliensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus baoshanensis (Zhang, Ji, Yang & Chen, 2011). Asia-Pacific. Non-pest.

Zeugodacus biguttatus (Bezzi, 1916). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus binoyi (Drew, 2002). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus bogorensis (Hardy, 1983). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus borongensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus brachus (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus brevipunctatus (David & Hancock, 2017), comb. n. Asia-Pacific. Non-pest. Cue-lure.

Notes: This species was recently described in *Bactrocera* and placed in the subgenus *Sinodacus*, of which all other previous members have been transferred to *Zeugodacus* (De Meyer et al. 2015). We here follow this reasoning.

Zeugodacus brevivitta (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus buruensis (White, 1999). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus buvittatus (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus calumniatus (Hardy, 1970). Asia-Pacific. Non-pest. Methyl eugenol.

Zeugodacus careomacula (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus caudatus (Fabricius, 1805). Asia-Pacific. Cucurbitaceae flower pest. Cue-lure. Notes: Type species for genus.

Zeugodacus choristus (May, 1962). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus cilifer (Hendel, 1912). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus citrifuscus (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus citroides (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus complicatus (White, 1999). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus connexus (Hardy, 1982). Asia-Pacific. Non-pest.

Zeugodacus cucumis (French, 1907). Asia-Pacific. Cucurbitaceae fruit pest.

Zeugodacus cucurbitae (Coquillett, 1899). Asia-Pacific. Cucurbitaceae fruit pest. Cuelure, zingerone.

Notes: *Zeugodacus cucurbitae*, the melon fly, is one of the most significant pest species with the Tephritidae. Although different forms are recognized that can be correlated with different hosts, these are generally not thought to represent different (cryptic) species (De Meyer et al. 2015, Hendrichs et al. 2015). Natively wide-spread in Asia and invasive in many Pacific islands and the Afrotropical region.

Zeugodacus curtus (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus daclaciae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus daulus (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus decipiens (Drew, 1972). Asia-Pacific. Cucurbitaceae fruit pest.

Zeugodacus depressus (Shiraki, 1933). Asia-Pacific. Cucurbitaceae fruit pest.

Zeugodacus diaphoropsis (Hering, 1952). Asia-Pacific. Non-pest.

Zeugodacus diaphorus (Hendel, 1915). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus dissidens (Drew, 1989). Asia-Pacific. Non-pest.

Zeugodacus disturgidus (Yu, Deng & Chen, 2012). Asia-Pacific. Non-pest. Notes: Z. disturgidus is not included in the Drew and Romig (2013, 2016) keys. According to the diagnosis, it is similar to Z. vinnulus but differs in having the face with two bands, and the costal band on the wing confluent with vein R₂₊₃ and not expanded apically.

Zeugodacus diversus (Coquillett, 1904). Asia-Pacific. Cucurbitaceae flower pest. Methyl eugenol.

Notes: Drew and Romig (2013) state that this species appears to have a weak attraction to methyl eugenol. We hereby confirm this attraction, based on the recent capture of fifteen flies among eight different trapping locations in Nepal and additional records from Bangladesh.

Zeugodacus dorsirufus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus dubiosus (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus duplicatus (Bezzi, 1916). Asia-Pacific. Non-pest.

Zeugodacus elegantulus (Hardy, 1974). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus emarginatus (Perkins, 1939). Asia-Pacific. Non-pest.

Zeugodacus emittens (Walker, 1860). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus eurylomatus (Hardy, 1982). Asia-Pacific. Non-pest.

Zeugodacus exornatus (Hering, 1941). Asia-Pacific. Non-pest. Cue-lure

Zeugodacus fallacis (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus fereuncinatus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus flavipilosus (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus flavolateralis (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus flavopectoralis (Hering, 1953). Asia-Pacific. Non-pest.

Zeugodacus flavoverticalis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus freidbergi (White, 1999). Asia-Pacific. Non-pest.

Zeugodacus fulvipes (Perkins, 1938). Asia-Pacific. Non-pest.
Zeugodacus fulvoabdominalis (White & Evenhuis, 1999). Asia-Pacific. Non-pest.
Zeugodacus fuscipennulus (Drew & Romig, 2001). Asia-Pacific. Non-pest.
Zeugodacus fuscoalatus (Drew & Romig, 2013). Asia-Pacific. Non-pest.
Zeugodacus gavisus (Munro, 1935). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus gracilis (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hamaceki (Drew & Romig, 2001). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hamaceki (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
Zeugodacus hatyaiensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus hekouanus (Yu He & Yang, 2011). Asia-Pacific. Non-pest. Zeugodacus hengsawadae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Zeugodacus hoabinhiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure Zeugodacus hochii (Zia, 1936). Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure, zingerone.

Notes: Zingerone is a new lure record. Zeugodacus hodgsoniae (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus hoedi (White, 1999). Asia-Pacific. Non-pest.

Zeugodacus hululangatiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus incisus (Walker, 1861). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus indentus (Hardy, 1974). Asia-Pacific. Non-pest.

Zeugodacus infestus (Enderlein, 1920). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus iriomotiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Methyl eugenol.

Zeugodacus ishigakiensis (Shiraki, 1933). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus isolatus (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus javadicus (Mahmood, 1999). Asia-Pacific. Non-pest.

Zeugodacus javanensis (Perkins, 1938), comb. n. Asia-Pacific. Non-pest.

Notes: Originally described in *Afrodacus*, here transferred from *Bactrocera*. It is placed in the subgenus *Javadacus*. Members of *Javadacus* were not moved to *Zeugo-dacus* by De Meyer et al. (2015) because only one representative, *B. unirufa* Drew, 1989, had been included in any molecular phylogenetic studies, where it was robustly placed in *Bactrocera*. However, *B. unirufa* has since been synonymized with *B. melanothoracica* and removed from *Javadacus* along with several other species that did not have the shallow posterior emargination of sternite V and elongate posterior surstylus lobes in the male genitalia, which fit *Zeugodacus*. We therefore now move all remaining species in the subgenus *Javadacus* to *Zeugodacus*.

Zeugodacus juxtuncinatus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus kaghanae (Mahmood, 1999). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus khaoyaiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus laguniensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus lipsanus (Hendel, 1915). Asia-Pacific. Non-pest.

Zeugodacus liquidus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus longicaudatus (Perkins, 1938). Asia-Pacific. Non-pest. Cue-lure. Zeugodacus longivittatus (Chua & Ooi, 1998). Asia-Pacific. Non-pest. Methyl eugenol. Zeugodacus luteicinctutus (Ito, 2011). Asia-Pacific. Non-pest.

Notes: *Z. luteicinctutus* is not included in the Drew and Romig (2013, 2016) keys. According to the diagnosis it is similar to *Z. yoshimotoi*, but differs in having dull brownish instead of shining a black marking surrounding the ocellar triangle. This may prove to be a junior synonym of *Z. yoshimotoi* when more specimens are studied or when molecular data become available.

Zeugodacus macrophyllae (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus macrovittatus (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus maculatus (Perkins, 1938). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus maculifacies (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus maculifemur (Hering, 1938). Asia-Pacific. Non-pest.

Zeugodacus magnicauda (White & Evenhuis, 1999). Asia-Pacific. Non-pest.

Zeugodacus melanofacies (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus melanopsis (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus menglanus (Yu Liu & Yang, 2011). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus mesonotaitha (Drew, 1989). Asia-Pacific. Non-pest.

Zeugodacus minimus (Hering, 1952). Asia-Pacific. Non-pest.

Zeugodacus montanus (Hardy, 1983), comb. nov. Asia-Pacific. Non-pest. Cue-lure. Notes: Originally described in *Dacus*, here transferred from *Bactrocera*. See further comments under *Z. javanensis*.

Zeugodacus mukiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus mundus (Bezzi, 1919). Asia-Pacific. Cucurbitaceae fruit pest.

Zeugodacus nakhonnayokiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure. Zeugodacus namlingiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus neoelegantulus (White, 1999). Asia-Pacific. Non-pest.

Zeugodacus neoemittens (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus neoflavipilosus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus neolipsanus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus neopallescentis (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus nigrifacies (Shiraki, 1933). Asia-Pacific. Non-pest.

Zeugodacus ochrosterna (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus okunii (Shiraki, 1933). Asia-Pacific. Non-pest.

Zeugodacus pahangiae (Drew & Romig, 2013). Asia-Pacific. Non-pest.

Zeugodacus pantabanganiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure. Zeugodacus papuaensis (Malloch 1939), comb. nov. Asia-Pacific. Non-pest.

Notes: This species was moved from *Dacus* to the subgenus *Austrodacus* by Hancock and Drew (2016), but they continued to classify that subgenus in *Bactrocera*. Like

all members of the subgenus *Austrodacus*, we here place it in the genus *Zeugodacus*. *Zeugodacus paululus* (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus pemalangiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure. *Zeugodacus perplexus* (Walker, 1862). Asia-Pacific. Non-pest.

- Zeugodacus perpusillus (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus persignatus (Hering, 1941). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus platamus (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus proprescutellatus (Zhang Che & Gao, 2011). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus pubescens (Bezzi, 1919). Asia-Pacific. Non-pest.
- Zeugodacus purus (White, 1999). Asia-Pacific. Non-pest.
- Zeugodacus quasiinfestus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus reflexus (Drew, 1971). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus rubellus (Hardy, 1973). Asia-Pacific. Non-pest.
- Zeugodacus sabahensis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus sandaracinus (Drew, 1989). Asia-Pacific. Non-pest.
- Zeugodacus sasaotiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus scutellaris (Bezzi, 1913). Asia-Pacific. Cucurbitaceae flower pest. Cue-lure.
- Zeugodacus scutellarius (Bezzi, 1916), comb. nov. Asia-Pacific. Non-pest. Cue-lure.
 - Notes: Originally described in *Chaetodacus*, here transferred from *Bactrocera*. See further comments under *Z. javanensis*.
- Zeugodacus scutellatus (Hendel, 1912). Asia-Pacific. Cucurbitaceae flower pest. Cue-lure. Zeugodacus scutellinus (Bezzi, 1916). Asia-Pacific. Non-pest.
- Zeugodacus semisurstyli (Drew & Romig, 2013), comb. nov. Asia-Pacific. Non-pest. Cue-lure.
- Notes: Here transferred from *Bactrocera*. See further comments under *Z. javanensis*. *Zeugodacus semongokensis* (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus sepikae (Drew, 1989). Asia-Pacific. Non-pest.
- Zeugodacus signatifer (Tryon, 1927). Asia-Pacific. Non-pest.
- Zeugodacus signatus (Hering, 1941). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus sinensis (Yu Bai & Chen, 2011). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus singularis (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus sonlaiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus speciosus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus spectabilis (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus strigifinis (Walker, 1861). Asia-Pacific. Cucurbitaceae flower pest. Cue-lure.
- Zeugodacus sumbensis (Hering, 1953). Asia-Pacific. Non-pest.
- Zeugodacus surrufulus (Drew, 1989). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus synnephes (Hendel, 1913). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus tapervitta (Mahmood, 1999). Asia-Pacific. Cucurbitaceae fruit pest.
- Zeugodacus tappanus (Shiraki, 1933). Asia-Pacific. Non-pest.
- Zeugodacus tau (Walker, 1849). Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure.
 - Notes: *Zeugodacus tau* possibly represents a cryptic species complex the extent of which is currently unclear (Baimai 2000, Kitthawee and Dujardin 2010, Kitthawee and Rungsri 2011, Dujardin and Kitthawee 2013).
- Zeugodacus tebeduiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus timorensis (Perkins, 1939). Asia-Pacific. Non-pest. Cue-lure.

Zeugodacus transversus (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.

- Zeugodacus triangularis (Drew, 1968). Asia-Pacific. Cucurbitaceae flower pest. Cuelure, zingerone.
- Zeugodacus trichosanthes (Drew & Romig, 2013). Asia-Pacific. Cucurbitaceae fruit pest. Cue-lure.
- Zeugodacus trichotus (May, 1962). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus tricuspidatae (Drew & Romig, 2013). Asia-Pacific. Non-pest.
- Zeugodacus trilineatus (Hardy, 1955), comb. nov. Asia-Pacific. Non-pest. Cue-lure.
 - Notes: Originally described in *Dacus*, here transferred from *Bactrocera*. See further comments under *Z. javanensis*.
- Zeugodacus trimaculatus (Hardy & Adachi, 1954). Asia-Pacific. Cucurbitaceae fruit pest. Zeugodacus trivandrumensis (Drew & Romig, 2013). Asia-Pacific. Non-pest.
- Zeugodacus ujungpandangiae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus uncinatus (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus unilateralis (Drew, 1989). Asia-Pacific. Non-pest.
- Zeugodacus univittatus (Drew, 1972). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus urens (White, 1999). Asia-Pacific. Non-pest.
- Zeugodacus vargus (Hardy, 1982). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus vinnulus (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus vultus (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure
- Zeugodacus waimitaliae (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus watersi (Hardy, 1954). Asia-Pacific. Non-pest.
- Zeugodacus whitei (Drew & Romig, 2013). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus yalaensis (Drew & Romig, 2013). Asia-Pacific. Non-pest.
- Zeugodacus yoshimotoi (Hardy, 1973). Asia-Pacific. Non-pest. Cue-lure.
- Zeugodacus zahadi (Mahmood, 1999). Asia-Pacific. Non-pest. Cue-lure.
 - Notes: The characters that supposedly distinguish *Z. zahadi* from *Z. tau* overlap, and *Z. zahadi* may be a synonym of *Z. tau* (Drew & Romig, 2013). See further notes under *Z. tau*.

Acknowledgements

We would like to thank Ho-Yeon Han, one anonymous reviewer, and the editor for their comments, which helped to improve the manuscript. This research was funded in part by the College of Tropical Agriculture and Human Resources, University of Hawaii, at Manoa, the USDA Cooperative State Research, Education and Extension (CSREES) project HAW00942-H administered by the College of Tropical Agriculture and Human Resources, University of Hawaii, and the USDA Farm Bill grant, FY17 3.0497.01. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement. USDA is an equal opportunity provider and employer.

References

- Baimai V (2000) Cytological evidence for a complex of species within the taxon *Bactrocera tau* (Diptera: Tephritidae) in Thailand. Biological Journal of the Linnean Society 69: 399–409. https://doi.org/10.1006/bijl.1999.0377
- CABI (2017) Invasive Species Compendium. http://www.cabi.org/isc/ [accessed Oct. 2017]
- Cameron EC, Sved JA, Gilchrist AS (2010) Pest fruit fly (Diptera: Tephritidae) in northwestern Australia: One species or two? Bulletin of Entomological Research 100: 197–206. https://doi.org/10.1017/S0007485309990150
- Clarke AR, Armstrong KF, Carmichael AE, Milne JR, Raghu S, Roderick GK, Yeates DK (2005) Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis* complex of fruit flies. Annual Review of Entomology 50: 293–319. https://doi.org/10.1146/annurev.ento.50.071803.130428
- David KJ, Hancock DL, Singh SK, Ramani S, Behere GT, Salini S (2017) New species, new records and updated subgeneric key of *Bactrocera* Macquart (Diptera: Tephritidae: Dacinae: Dacini) from India. Zootaxa 4272: 386–400. https://doi.org/10.11646/zootaxa.4272.3.4
- David KJ, Ramani S, Whitmore D, Ranganath HR (2016) Two new species and a new record of *Bactrocera* Macquart (Diptera: Tephritidae: Dacinae: Dacini) from India. Zootaxa 4103: 25–34. https://doi.org/10.11646/zootaxa.4103.1.2
- De Meyer M, Delatte H, Mwatawala M, Quilici S, Vayssières JF, Virgilio M (2015) A review of the current knowledge on *Zeugodacus cucurbitae* (Coquillett) (Diptera, Tephritidae) in Africa, with a list of species included in *Zeugodacus*. ZooKeys 540: 539–557 + Supplementary material 1:(4). https://doi.org/10.3897/zookeys.540.9672
- De Meyer M, White I (2016) True Fruit Flies (Diptera, Tephritidae) of the Afrotropical Region. http://projects.bebif.be/fruitfly/index.html [accessed Oct. 2017]
- Drew RAI (1971) New species of Dacinae (Diptera: Trypetidae) from the South Pacific Area. Queensland Journal of Agricultural Science 28: 29–103.
- Drew RAI (1989) The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian Regions. Memoirs of the Queensland Museum 1: 1–536.
- Drew RAI, Hancock DL (1994) The Bactrocera dorsalis complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. Bulletin of Entomological Research Supplement Series 2: 1–68. https://doi.org/10.1017/S1367426900000278
- Drew RAI, Hancock DL (2016) A review of the subgenus Bulladacus Drew & Hancock of Bactrocera Macquart (Diptera: Tephritidae: Dacinae), with description of two new species from Papua New Guinea. Australian Entomologist 43: 189–210.
- Drew RAI, Ma J, Smith S, Hughes JM (2011) The taxonomy and phylogenetic relationships of species in the *Bactrocera musae* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Papua New Guinea. Raffles Bulletin of Zoology 59: 145–162.
- Drew RAI, Romig MC (2013) Tropical fruit flies of South-East Asia. CABI, Wallingford, 655 pp.
- Drew RAI, Romig MC (2016) Keys to the Tropical Fruit Flies of South-East Asia. CABI, Wallingford, 487 pp.
- Dujardin JP, Kitthawee S (2013) Phenetic structure of two Bactrocera tau cryptic species (Diptera: Tephritidae) infesting Momordica cochinchinensis (Cucurbitaceae) in Thailand and Laos. Zoology 116: 129–138. https://doi.org/10.1016/j.zool.2012.07.004

- Dupuis JR, Bremer FT, Kauwe A, San Jose M, Leblanc L, Rubinoff D, Geib S (2017) HiMAP: Robust phylogenomics from highly multiplexed amplicon sequencing. bioRxiv. http://biorxiv.org/content/early/2017/11/05/213454.abstract
- Ebina T, Ohto K (2006) Morphological characters and PCR-RFLP markers in the interspecific hybrids between *Bactrocera carambolae* and *B. papayae* of the *B. dorsalis* species complex (Diptera: Tephritidae). Research Bulletin of the Plant Protection Service, Japan 42: 23–34.
- Ekesi S, De Meyer M, Mohamed SA, Virgilio M, Borgemeister C (2016) Taxonomy, ecology, and management of native and exotic fruit fly species in Africa. Annual Review of Entomology 61: 219–238. https://doi.org/10.1146/annurev-ento-010715-023603
- Fay HAC (2012) A highly effective and selective male lure for *Bactrocera jarvisi* (Tryon) (Diptera: Tephritidae). Australian Journal of Entomology 51: 189–197. https://doi. org/10.1111/j.1440-6055.2011.00847.x
- Fletcher B (1987) The biology of Dacine fruit flies. Annual Review of Entomology 32: 115–144. https://doi.org/10.1146/annurev.ento.32.1.115
- Freidberg A, Kovac D, Shiao S (2017) A revision of *Ichneumonopsis* Hardy, 1973 (Diptera: Tephritidae: Dacinae: Gastrozonini), Oriental bamboo-shoot fruit flies. European Journal of Taxonomy 317: 1–23. https://doi.org/10.5852/ejt.2017.317
- Gilchrist AS, Wang Y, Yu H, Raphael K (2003) Genetic delineation of sibling species of the pest fruit fly *Bactocera* (Diptera: Tephritidae) using microsatellites. Bulletin of Entomological Research 93: 351–360. https://doi.org/10.1079/BER2003249
- Han H-Y, Choi D-S, Ro K-E (2017) Taxonomy of Korean *Bactrocera* (Diptera: Tephritidae: Dacinae) with review of their biology. Journal of Asia-Pacific Entomology 20: 1321–1332. https://doi.org/10.1016/j.aspen.2017.09.011
- Hancock DL (2015) A new subgenus for six Indo-Australian species of *Bactrocera* Macquart (Diptera: Tephritidae: Dacinae) and subgeneric transfer of four other species. Australian Entomologist 42: 39–44.
- Hancock DL, Hamacek EL, Lloyd AC, Elson-Harris MM (2000) The distribution and host plants of fruit flies (Diptera: Tephritidae) in Australia. Information Series QI99067, Queensland Department of Primary Industries, Brisbane, 75 pp.
- Hancock DL, Drew RAI (2006) A revised classification of subgenera and species groups in *Dacus* Fabricius (Diptera: Tephritidae). Instrumenta Biodiversitatis 7: 167–205.
- Hancock DL, Drew RAI (2015) A review of the Indo-Australasian subgenus *Parazeugodacus* Shiraki of *Bactrocera* Macquart (Diptera: Tephritidae: Daciniae). Australian Entomologist 42: 91–104.
- Hancock DL, Drew RAI (2017a) A review of the subgenus *Javadacus* Hardy of *Bactrocera* Macquart (Diptera: Tephritidae: Dacinae). Australian Entomologist 44: 105–112.
- Hancock DL, Drew RAI (2017b) A review of the Indo-Australian subgenera *Heminotodacus* Drew, *Paradacus* Perkins and *Perkinsidacus* subgen. n. of *Bactrocera* Macquart (Diptera: Tephritidae: Dacinae). Australian Entomologist 44: 137–146.
- Hardy DE (1954) The *Dacus* subgenera *Neodacus* and *Gymnodacus* of the world (Diptera, Tephritidae). Proceedings of the Entomological Society of Washington 56: 5–23.
- Hardy DE (1955) A reclassification of the Dacini (Tephritidae-Diptera). Annals of the Entomological Society of America 48: 1–13. https://doi.org/10.1093/aesa/48.6.425

- Hardy DE (1976) Resurrection of *Bactrocera* Macquart and clarification of the type-species, *longicornis* Macquart (Diptera: Tephritidae). Proceedings of the Hawaiian Entomological Society 22: 245–249.
- Hendel FG (1927) Einige neue Bohrfliegen (Trypetidae) aus dem Hamburger Museum. Wiener Entomologische Zeitung 44: 58–65.
- Hendrichs J, Vera MT, De Meyer M, Clarke AR (2015) Resolving cryptic species complexes of major tephritid pests. ZooKeys 540: 5–39. https://doi.org/10.3897/zookeys.540.9656
- International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature. Fourth edition. In: Ride WDL et al. (Eds) The International Trust for Zoological Nomenclature, London, 306 pp. http://www.nhm.ac.uk/hosted-sites/iczn/code/
- Ito S (2011) Die Bohrfliegen aus Nordost-Nepal (Diptera, Tephritidae). Esakia 51: 1-45.
- Kitthawee S, Dujardin JP (2010) The geometric approach to explore the *Bactrocera tau* complex (Diptera: Tephritidae) in Thailand. Zoology 113: 243–249. https://doi.org/10.1016/j. zool.2009.12.002
- Kitthawee S, Rungsri N (2011) Differentiation in wing shape in the *Bactrocera tau* (Walker) complex on a single fruit species of Thailand. ScienceAsia 37: 308–313. https://doi.org/10.2306/scienceasia1513-1874.2011.37.308
- Krosch MN, Schutze MK, Armstrong KF, Graham GC, Yeates DK, Clarke AR (2012) A molecular phylogeny for the Tribe Dacini (Diptera: Tephritidae): systematic and biogeographic implications. Molecular Phylogenetics and Evolution 64: 513–523. https://doi.org/10.1016/j.ympev.2012.05.006
- Leblanc L, San Jose M, Rubinoff D (2015a) Description of a new species and new country distibution records of *Bactrocera* (Diptera: Tephritidae: Dacinae) from Cambodia. Zootaxa 4012: 593–600. https://doi.org/10.11646/zootaxa.4012.3.12
- Leblanc L, San Jose M, Barr N, Rubinoff D (2015b) A phylogenetic assessment of the polyphyletic nature and intraspecific color polymorphism in the *Bactrocera dorsalis* complex (Diptera, Tephritidae). ZooKeys 540: 339–367. https://doi.org/10.3897/zookeys.540.9786
- Manrakhan A, Daneel JH, Beck R, Virgilio M, Meganck K, De Meyer M (2017) Efficacy of trapping systems for monitoring of Afrotropical fruit flies. Journal of Applied Entomology. https://doi.org/10.1111/jen.12373
- Munro HK (1984) A taxonomic treatise on the Dacidae (Tephritoidea, Diptera) of Africa. Entomology Memoirs, Department of Agriculture and Water Supply, Republic of South Africa 61: 1–313.
- Nakahara SMM, Muraji M (2008) Phylogenetic analyses of *Bactrocera* fruit flies (Diptera: Tephritidae) based on nucleotide sequences of the mitochondrial COI and COII genes. Research Bulletin of the Plant Protection Service Japan 44: 1–12.
- Norrbom AL, Carroll LE, Thompson FC, White IM, Freidberg A (1999) Systematic Database of Names. In: Thompson FC (Ed.) Fruit fly expert identification system and systematic information database. Myia (1998) 9: 65–251, & Diptera Data Dissemination Disk (CD-ROM) (1998) 1.
- Norrbom AL (2004) Updates to Biosystematic Database of World Diptera for Tephritidae through 1999. Diptera Data Dissemination Disk (CD-ROM) 2.
- Pape T, Blagoderov V, Mostovski MB (2011) Order DIPTERA Linnaeus, 1758. Zootaxa 3148: 222–229.

- Pape T, Thompson FC (Eds) (2013) Systema Diptorum, Version 1.5. http://diptera.org/ [accessed on Oct. 2018]
- Pest Management in the Pacific Project (2003) Pacific Fruit Fly Project. https://lrd.spc.int/ pacific-fruit-fly [accessed on Oct. 2017]
- Roskov Y, Abucay L, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, De Wever A, Nieukerken EJ van, Zarucchi J, Penev L (2017) Species 2000 & ITIS Catalogue of Life, 2017 Annual Checklist. Digital resource at www.catalogueoflife.org/ annual-checklist/2017. Species 2000: Naturalis, Leiden, the Netherlands. http://projects. bebif.be/fruitfly/index.html
- Royer JE (2015) Responses of fruit flies (Tephritidae: Dacinae) to novel male attractants in north Queensland, Australia, and improved lures for some pest species. Austral Entomology 54: 411–426. https://doi.org/10.1111/aen.12141
- Royer JE, Agovaua S, Bokosou J, Kurika K, Mararuai A, Mayer DG, Niangu B (2017) Responses of fruit flies (Diptera: Tephritidae) to new attractants in Papua New Guinea. Austral Entomology. https://doi.org/10.1111/aen.12269
- San Jose M, Doorenweerd C, Leblanc L, Barr N, Geib SM, Rubinoff D (2018) Incongruence between molecules and morphology: A seven-gene phylogeny of Dacini fruit flies paves the way for reclassification (Diptera: Tephritidae). Molecular Phylogenetics and Evolution. https://doi.org/10.1016/j.ympev.2017.12.001
- San Jose M, Leblanc L, Rubinoff D (2013) An evaluation of the species status of *Bactrocera in-vadens* and the systematics of the *Bactrocera dorsalis* (Diptera: Tephritidae) complex. Annals of the Entomological Society of America 106: 684–694. https://doi.org/10.1603/AN13017
- Schutze MK, Aketarawong N, Amornsak W, Armstrong KF, Augustinos AA, Barr N, Bo W, Bourtzis K, Boykin LM, Cáceres C, Cameron SL, Chapman TA, Chinvinijkul S, Chomic A, De Meyer M, Drosopoulou E, Englezou A, Ekesi S, Gariou-Papalexiou A, Geib SM, Hailstones D, Hasanuzzaman M, Haymer D, Hee AKW, Hendrichs J, Jessup A, Ji Q, Khamis FM, Krosch MN, Leblanc LUC, Mahmood K, Malacrida AR, Mavragani-Tsipidou P, Mwatawala M, Nishida R, Ono H, Reyes J, Rubinoff D, San Jose M, Shelly TE, Srikachar S, Tan KH, Thanaphum S, Haq I, Vijaysegaran S, Wee SL, Yesmin F, Zacharopoulou A, Clarke AR (2015a) Synonymization of key pest species within the *Bactrocera dorsalis* species complex (Diptera: Tephritidae): Taxonomic changes based on a review of 20 years of integrative morphological, molecular, cytogenetic, behavioural and chemoecological data. Systematic Entomology 40: 456–471. https://doi.org/10.1111/syen.12113
- Schutze MK, Mahmood K, Pavasovic A, Bo W, Newman J, Clarke AR, Krosch MN, Cameron SL (2015b) One and the same: Integrative taxonomic evidence that *Bactrocera invadens* (Diptera: Tephritidae) is the same species as the Oriental fruit fly *Bactrocera dorsalis*. Systematic Entomology 40: 472–486. https://doi.org/10.1111/syen.12114
- Schutze MK, Virgilio M, Norrbom A, Clarke AR (2017) Tephritid integrative taxonomy: Where we are now, with a focus on the resolution of three tropical fruit fly species complexes. Annual Review of Entomology 62: 147–164. https://doi.org/10.1146/annurev-ento-031616-035518
- Smith PT, Kambhampati S, Armstrong KA (2003) Phylogenetic relationships among *Bactrocera* species (Diptera: Tephritidae) inferred from mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 26: 8–17. https://doi.org/10.1016/S1055-7903(02)00293-2

- Tan KH, Nishida R (2000) Mutual reproductive benefits between a wild orchid, Bulbophyllum patens, and Bactrocera fruit flies via a floral synomone. Journal of Chemical Ecology 26: 533–546. https://doi.org/10.1023/A:1005477926244
- Vargas RI, Pinero JC, Leblanc L (2015) An overview of pest species of *Bactrocera* fruit flies (Diptera: Tephritidae) and the integration of biopesticides with other biological approaches for their management with a focus on the Pacific region. Insects 6: 297–318. https://doi.org/10.3390/insects6020297
- Virgilio M, Jordaens K, Verwimp C, White IM, De Meyer M (2015) Higher phylogeny of frugivorous flies (Diptera, Tephritidae, Dacini): Localised partition conflicts and a novel generic classification. Molecular Phylogenetics and Evolution 85: 171–179. https://doi. org/10.1016/j.ympev.2015.01.007
- White IM (1999) Morphological features of the Tribe Dacini (Dacinae): Their significance to behavior and classification. In: Aluja M, Norrbom AL (Eds) Fruit Flies (Tephritidae): Phylogeny and evolution of Behavior. CRC Press, Boca Raton, 505–534. https://doi. org/10.1201/9781420074468.ch20
- White IM (2006) Taxonomy of the Dacina (Diptera:Tephritidae) of Africa and the Middle East. African Entomology Memoir 2: 1–156.
- White IM, Headrick DH, Norrbom AL, Carroll LE (1999) Glossary. In: Aluja M, Norrbom AL (Eds) Fruit flies (Tephritidae): Phylogeny and evolution of behavior. CRC Press, Boca Raton, 881–924. https://doi.org/10.1201/9781420074468.sec8
- White IM, Elson-Harris MM (1992) Fruit flies of economic significance. CABI, Wallingford, 601 pp.
- Whitman DW, Orsak L, Greene E (1988) Spider mimicry in fruit flies (Diptera: Tephritidae): Further experiments on the deterrence of jumping spiders (Araneae: Salticidae) by Zonosemata vittigera (Coquillett). Annals of the Entomological Society of America 81: 532–536. http://dx.doi.org/10.1093/aesa/81.3.532
- Yu H, Deng Y-L, Chen N-Z (2012) A new species of the subgenus Sinodacus from Yunnan, China (Diptera, Tephritidae). Acta Zootaxonomica Sinica 37: 834–836.
- Zhang Z-Q (2011) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 1–237.

Supplementary material I

A global checklist of the 932 fruit fly species in the tribe Dacini (Diptera: Tephritidae), spreadsheet table.

Authors: Camiel Doorenweerd, Luc Leblanc, Allen L. Norrbom, Michael San Jose, Daniel Rubinoff

Data type: Checklist

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.730.21786.suppl1

CHECKLIST



Updated checklist of the Michigan (USA) caddisflies, with regional and habitat affinities

David C. Houghton¹, R. Edward DeWalt², Angelica J. Pytel¹, Constance M. Brandin¹, Sarah E. Rogers¹, David E. Ruiter³, Ethan Bright⁴, Patrick L. Hudson⁵, Brian J. Armitage⁶

I Department of Biology, Hillsdale College, 33 East College Street, Hillsdale, MI 49242, USA 2 Illinois Natural History Survey, 1816 South Oak Street, Champaign IL 61820, USA 3 235 SW Central Avenue, Grants Pass, OR 97526, USA 4 Museum of Zoology, University of Michigan, Ann Arbor, MI 48103, USA 5 Great Lakes Science Center, US Geological Survey, 1451 Green Road, Ann Arbor, MI 48105, USA 6 Instituto Conmemorativo Gorgas de Estudio de la Salud, Ave. Justo Arosemena y Calle 35, Apartado Postal No 0816-02593, Ciudad de Panamá, Republic of Panamá

Corresponding author: David C. Houghton (david.houghton@hillsdale.edu)

Academic editor: A. Previši	č Received 20 October 2017	Accepted 6 December 2017	Published 17 January 2018
	http://zoobank.org/D8CA634C-3E	D1-49E4-92E5-C91DFFB327E3	;

Citation: Houghton DC, DeWalt RE, Pytel AJ, Brandin CM, Rogers SE, Ruiter DE, Bright E, Hudson PL, Armitage BJ (2018) Updated checklist of the Michigan (USA) caddisflies, with regional and habitat affinities. ZooKeys 730: 57–74. https://doi.org/10.3897/zookeys.730.21776

Abstract

Based on examination of ~180,000 specimens from 695 collections of 443 localities collected from the 1930s to 2015 we report 295 species of caddisflies from Michigan. Of these, 41 are reported from the state for the first time. Another 18 species previously reported from Michigan are listed as doubtful. The 11 most abundant species collectively represented over half of all specimens collected. Conversely, 80 species were known from <10 specimens, and 27 species from a single specimen. The Michigan fauna is similar to those of Minnesota and Ohio, adjacent states with comparable recent collecting effort. Regional and habitat affinities for each Michigan species are reported herein. Due to the high level of species discovery over the last few years, despite a >80-year collecting history, it is likely that additional species remain undiscovered in the state.

Keywords

Michigan, Trichoptera, caddisfly, checklist, species, diversity

Introduction

Despite the ecological importance of caddisflies in aquatic ecosystems and their utility in biological monitoring (Barbour et al. 1999), the faunas of the northcentral U.S. and southcentral Canada are not well known. Only the faunas of Illinois (Ross 1944), Minnesota (Houghton 2012), and Ohio (Armitage et al. 2011) have been extensively studied. For the remainder of the region, basic species checklists have been compiled for the Indiana (Waltz and McCafferty 1983), Manitoba (Flannagan and Flannagan 1982), Michigan (Leonard and Leonard 1949b), North Dakota (Harris et al. 1980), and Wisconsin (Longridge and Hilsenhoff 1973) caddisflies. All of these studies are >30 years old, and it is difficult to ascertain if changes to the fauna have occurred during the interim.

The caddisflies of Michigan are known on a species level primarily from Leonard and Leonard's (1949b) checklist. A compilation of known and suspected species is maintained by Bright (2017). The overall caddisfly distributions of the state have been divided into three distinct regions corresponding to the Northern Great Lakes, Northern Forested, and Southern Agricultural regions (Houghton 2015) (Figure 1). Many additional state records have been reported during the last 20 years (Table 1), but no comprehensive inventory of the state has occurred since the 1940s. Thus, the objectives of our study were to inventory the state and compile a comprehensive checklist of the Michigan fauna, and to relate this fauna to the three established caddisfly regions and different types of aquatic habitats.

Materials and methods

We have been collecting caddisflies in Michigan since the 1990s, primarily using ultraviolet light traps for adults. Other adult collecting methods have included malaise trapping, sweep netting, and aspirating from riparian rocks and vegetation. Larval collection

Table 1. Past faunal studies of Michigan caddisflies, with resulting numbers of specimens, reported species, and new state records. Nearly all of the specimens associated with these studies were examined during the current study.

Reference	Region	Specimens	Species	State records
Ross (1938, 1941, 1944, 1946)	statewide	?	101	101
Leonard and Leonard (1949a)	statewide	?	N/A	7
Leonard and Leonard (1949b)	statewide	5,767	181	66
Ellis (1962)	Houghton Creek	?	85	0
Davis et al. (1991)	St. Clair/Detroit River	?	70	21
Houghton et al. (2011)	Manistee River watershed	26,000+	134	11
DeWalt and South (2015)	Isle Royale National Park	326	42	2
Houghton (2016)	Black River Ranch	38,248	117	3
Current paper	statewide	~180,000	291	41



Figure 1. The determined caddisfly regions of Michigan (Houghton 2015), showing the collecting localities for this study.

methods included kick-netting, hand-picking, and Hess sampling. Most adult collecting took place during June and July, the peak emergence period of caddisflies in central Michigan (Houghton et al. 2011). Additional collections of adults were made during May, August, and September to obtain early and late emerging species.

Collecting sites were chosen to yield a geographically representative sample, paying particular attention to unique habitats, such as intermittent streams, waterfalls, and forested wetlands. We collected from sites that appeared to be the least disturbed of their general area. Unique areas, such as the Huron and Porcupine Mountains in the northeastern Upper Peninsula, the Black River Ranch in the northern Lower Peninsula, Sleeping Bear Dunes National Park in the northwestern Lower Peninsula, and Sarah Jane's Natural Area in the southern Lower Peninsula were sampled more intensively. Most notably, Fairbanks Creek, a pristine small stream in the northern Lower Peninsula, was sampled every week from May to October 2010–2014.

Specimens were identified using Houghton (2012) and more specific taxonomic treatments. Nomenclature follows that of Morse (2017). Most collected specimens and their respective locality data were databased using BIOTA software (Colwell 2007) and deposited in the Hillsdale College Insect Collection or the Illinois Natural History Survey. Some are in the personal collection of DER. Museum specimens from the University of Michigan were examined, especially records associated with Leonard and Leonard's (1949b) checklist. Specimens referenced in Table 1 were also examined. Additional records were located in collections of Brigham Young University, the University of Minnesota, and Colorado State University. These specimens remain in their respective institutions.

Results

Approximately 180,000 specimens from 695 collections of 443 Michigan localities from the 1930s to 2015 were examined during this study (Figure 1). From these specimens, we determined 295 total species, representing 20 families and 76 genera. Of these species, 41 are reported from Michigan for the first time and 204 are new since Leonard and Leonard's (1949b) checklist. These species are presented in Table 2, along with their regional and habitat affinities and the depository of specimens. An additional 18 species previously reported from Michigan are listed as doubtful due to synonymy, misidentification, or our inability to locate a specimen (Table 3).

Oecetis inconspicua (Walker) (Leptoceridae) was the most widespread species, followed by *Psychomyia flavida* Hagen (Psychomyiidae) and *Helicopsyche borealis* (Hagen) (Helicopsychidae) (Table 2). *Oecetis inconspicua* was also the most abundant species, followed by *P. flavida* and *Chimarra socia* (Hagen) (Philopotamidae). The 11 most abundant species collectively represented over half of all specimens collected. Conversely, 80 species were known from <10 specimens, and 27 species from a single specimen (Figure 2). Hydroptilidae (63 species), Limnephilidae (49), and Leptoceridae (46) were the most species-rich families; *Hydroptila* (28), *Hydropsyche* (21), and *Limnephilus* (20) the most species and the most species found exclusively in a single region, followed by the Northern Great Lakes and Southern Agricultural regions (Figure 3). Medium (4–15 m) rivers had the most total and unique species, followed by small (<4 m) streams, lakes, and large (>15 m) rivers.

Discussion

Nearly all of the species reported here are based on verified adult male specimens. The current location of these specimens is reported in Table 2. One exception is **Table 2.** The 295 caddisfly species confirmed from Michigan. Taxa are arranged alphabetically by family and genus. The number of species within each family is listed after each respective family. Species reported from Michigan for the first time are in boldface type. Collection data for each newly-reported species are included in Suppl. material 1. Spcs = total number of examined specimens, locs = total number of known localities. Dep. = museum with the largest number of deposited specimens. HCIC = Hillsdale College Insect Collection, INHS = Illinois Natural History Survey, UMMZ = University of Michigan Museum of Zoology, DER = personal collection of Dave Ruiter. NG = total specimens known from Northern Great Lakes caddisfly region, NF = total specimens from Northern Forested region, SA = total specimens from Southern Agricultural region (Figure 1). Lk = number of specimens known from lakes, SR = number of specimens from small (<4 m in width) rivers, MR = number of specimens from medium (4–15 m) rivers, LR = number of specimens from large (>15 m) rivers. Total number of species due to a lack of information about some collecting localities.

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
APATANIIDAE (1)										
Apatania zonella (Zetterstedt, 1840)	49	4	HCIC	49	0	0	18	0	0	31
BRACHYCENTRIDAE (8)										
Brachycentrus americanus (Banks, 1899)	3547	81	HCIC	1278	2218	51	6	1094	2343	60
B. fuliginosus Walker, 1852	25	6	UMMZ	0	25	0	0	0	25	0
B. incanus Hagen, 1861	1	1	INHS	1	0	0	0	0	1	0
B. lateralis (Say, 1823)	69	4	UMMZ	0	69	0	0	0	69	0
B. numerosus (Say, 1823)	122	21	UMMZ	9	72	41	0	56	34	31
Micrasema charonis Banks, 1914	5	2	INHS	0	2	3	0	0	2	3
M. rusticum (Hagen, 1868)	783	56	HCIC	24	722	37	4	97	669	13
M. wataga Ross, 1938	50	10	HCIC	40	10	0	0	3	44	3
DIPSEUDOPSIDAE (1)										
Phylocentropus placidus (Banks, 1905)	274	24	HCIC	235	17	21	71	86	104	3
GLOSSOSOMATIDAE (8)										
Agapetus hessi Leonard & Leonard, 1949	102	3	HCIC	0	102	0	0	0	102	0
A. tomus Ross, 1941	63	8	HCIC	27	0	36	0	12	49	0
Glossosoma intermedium Klapálek, 1892	16	9	HCIC	18	0	0	2	0	14	0
G. lividum (Hagen, 1861)	268	8	UMMZ	0	268	0	0	9	259	0
G. nigrior Banks, 1911	1796	68	HCIC	179	1575	42	22	1355	395	10
Protoptila erotica Ross, 1938	138	12	HCIC	4	130	4	1	0	63	74
P. maculata (Hagen, 1861)	76	10	HCIC	2	5	69	1	4	38	22
P. tenebrosa (Walker, 1852)	444	27	HCIC	223	220	1	6	197	223	18
GOERIDAE (1)										
Goera stylata Ross, 1938	2422	12	HCIC	30	2392	0	0	2361	58	3
HELICOPSYCHIDAE (1)										
Helicopsyche borealis (Hagen, 1861)	6957	114	HCIC	281	6347	310	1186	1703	3161	800
HYDROPSYCHIDAE (35)										
Arctopsyche ladogensis (Kolenati, 1859)	16	2	UMMZ	15	1	0	0	1	15	0
Cheumatopsyche analis (Banks, 1908)	1137	99	HCIC	334	485	318	80	263	625	53
C. aphanta Ross, 1938	38	2	HCIC	0	37	1	0	0	38	0
C. campyla Ross, 1938	6683	65	HCIC	55	257	6371	56	13	248	6312
C. gracilis (Banks, 1899)	1063	64	HCIC	248	804	11	2	33	912	114
C. minuscula (Banks, 1907)	2	1	HCIC	2	0	0	0	0	0	2

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
C. oxa Ross, 1938	1609	58	HCIC	69	1425	112	3	1077	516	8
C. pasella Ross, 1941	44	9	HCIC	6	37	1	2	1	41	0
C. sordida (Hagen, 1861)	7	4	HCIC	5	0	2	0	1	0	5
C. speciosa (Banks, 1904)	61	2	HCIC	0	0	61	0	0	0	58
Diplectrona modesta Banks, 1908	1106	9	HCIC	5	1096	5	0	1106	0	0
Hydropsyche aerata Ross, 1938	5	2	INHS	0	0	4	0	0	0	0
H. alhedra (Ross, 1939)	56	7	HCIC	15	40	1	0	5	49	2
H. alternans (Walker, 1852)	118	11	HCIC	115	2	1	57	2	0	54
H. arinale Ross, 1938	1	1	INHS	1	0	0	0	0	1	0
H. betteni Ross, 1938	1262	67	HCIC	74	1041	147	13	932	266	33
H. bronta (Ross, 1938)	192	43	HCIC	37	96	59	1	17	141	33
H. cheilonis (Ross, 1938)	17	8	HCIC	0	2	14	0	0	0	4
H. cuanis Ross, 1938	21	4	INHS	0	0	21	0	7	8	6
H. dicantha Ross, 1938	11	7	HCIC	1	6	2	0	2	6	1
H. frisoni Ross, 1938	73	11	INHS	1	36	32	0	0	67	3
H. incommoda Hagen, 1861	130	14	HCIC	1	12	116	1	2	13	74
H. leonardi Ross, 1938	2	1	INHS	0	2	0	0	0	2	0
H. morosa (Hagen, 1861)	262	32	HCIC	62	162	39	10	18	165	61
H. phalerata Hagen, 1861	31	5	HCIC	0	4	27	0	0	0	23
H. placoda Ross, 1941	1	1	HCIC	0	0	1	0	0	0	1
<i>H. scalaris</i> Hagen, 1861	3	3	INHS	0	0	2	0	0	0	0
H. simulans Ross, 1938	26	4	HCIC	0	22	4	3	0	3	16
H. slossonae (Banks, 1905)	1241	68	HCIC	137	1036	68	0	586	646	7
H. sparna (Ross, 1938)	2712	113	HCIC	425	2018	261	12	1253	1330	88
<i>H. vexa</i> (Ross, 1938)	12	6	HCIC	4	8	0	0	4	7	1
H. walkeri (Betten & Mosely, 1940)	65	13	HCIC	42	22	1	1	1	24	39
Macrostemum zebratum (Hagen, 1861)	533	15	HCIC	10	499	24	10	2	24	490
Parapsyche apicalis (Banks, 1908)	220	19	HCIC	62	252	6	1	274	45	0
Potamyia flava (Hagen, 1861)	119	16	HCIC	1	71	47	0	45	31	28
HYDROPTILIDAE (63)										
Agraylea multipunctata Curtis, 1834	4952	59	HCIC	127	927	3898	195	581	339	31
<i>Hydroptila ajax</i> Ross, 1938	27	3	HCIC	0	0	27	0	0	0	19
<i>H. albicornis</i> Hagen, 1861	1	1	HCIC	1	0	0	0	0	1	0
H. amoena Ross, 1938	8	4	HCIC	1	7	0	2	0	6	0
H. ampoda Ross, 1941	15	9	HCIC	15	0	0	0	0	15	0
H. angusta Ross, 1938	45	2	HCIC	0	0	45	0	0	0	45
<i>H. antennopedia</i> Sykora & Harris, 1994	111	9	HCIC	111	0	0	6	12	93	0
H. armata Ross, 1938	48	17	HCIC	6	13	29	2	2	40	1
H. berneri Ross, 1941	1	1	UMMZ	0	0	1	0	0	0	0
H. calia Denning, 1948	1	1	UMMZ	0	0	0	0	0	1	0
H. consimilis Morton, 1905	195	28	HCIC	31	140	24	0	62	129	4
H. delineata Morton, 1905	1	1	HCIC	1	0	0	0	0	1	0
H. grandiosa Ross, 1938	20	9	HCIC	0	9	11	0	1	9	1
H. hamata Morton, 1905	154	27	HCIC	46	100	8	62	5	75	4
<i>H. jackmanni</i> Blickle, 1963	477	37	HCIC	168	270	39	4	191	278	0
H. metoeca Blickle & Morse, 1954	166	16	HCIC	1	165	0	3	80	82	1
H. nicoli Ross, 1941	1	1	HCIC	1	0	0	0	0	1	0

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
H. novicola Blickle & Morse, 1954	1	1	HCIC	1	0	0	0	0	1	0
H. perdita Morton, 1905	11	6	HCIC	0	3	8	0	1	5	0
H. quinola Ross, 1947	3	2	HCIC	3	0	0	0	0	3	0
H. salmo Ross, 1941	1	1	HCIC	1	0	0	0	0	1	0
H. scolops Ross, 1938	18	2	UMMZ	0	16	2	0	0	16	0
H. spatulata Morton, 1905	9	5	HCIC	2	5	2	0	1	4	4
H. tortosa Ross, 1938	7	1	HCIC	0	7	0	0	0	7	0
H. tusculum Ross, 1947	1	1	HCIC	0	1	0	0	0	1	0
H. valhalla Denning, 1947	90	15	HCIC	88	2	0	0	2	87	1
H. waubesiana Betten, 1934	119	23	HCIC	7	36	76	8	17	51	3
H. wyomia Denning, 1948	23	5	HCIC	5	15	0	0	0	20	0
<i>H. xera</i> Ross, 1938	237	19	HCIC	189	51	0	2	1	235	2
Ithytrichia clavata Morton, 1905	222	6	HCIC	1	214	7	139	0	75	8
Leucotrichia pictipes (Banks, 1911)	30	2	HCIC	15	15	0	0	0	21	9
Mayatrichia ayama Mosely, 1905	7	2	UMMZ	0	6	1	0	0	6	0
Neotrichia halia Denning, 1948	131	3	HCIC	131	0	0	0	0	5	126
N. minutisimella (Chambers, 1873)	1	1	HCIC	1	0	0	0	0	0	1
N. okopa Ross, 1939	9	1	INHS	9	0	0	0	0	9	0
N. vibrans Ross, 1938	1	1	HCIC	0	1	0	0	0	0	1
Ochrotrichia arva (Ross, 1941)	3	2	HCIC	0	3	0	0	2	1	0
O. spinosa (Ross, 1938)	220	11	HCIC	209	4	7	7	46	161	6
<i>O. riesi</i> Ross, 1944	2	1	INHS	0	2	0	0	2	0	0
O. tarsalis (Hagen, 1861)	2	2	HCIC	1	0	1	0	0	2	0
Orthotrichia aegerfasciella (Chambers, 1873)	451	21	HCIC	1	64	386	38	5	54	5
O. balduffi Kingsolver & Ross, 1961	97	19	HCIC	11	42	44	25	2	36	4
O. cristata Morton, 1905	1813	49	HCIC	55	308	1450	163	71	187	0
O. curta Kingsolver & Ross, 1961	13	1	HCIC	13	0	0	13	0	0	0
Oxyethira aeola Ross, 1938	44	8	HCIC	0	44	0	0	5	39	0
O. anabola Blickle,1966	7	5	HCIC	5	2	0	0	1	4	2
O. araya Ross, 1941	1	1	HCIC	1	0	0	0	0	1	0
O. coercens Morton, 1905	115	19	HCIC	7	101	7	4	29	77	0
O. ecornuta Morton, 1893	73	3	HCIC	2	71	0	73	0	0	0
O. forcipata Mosely, 1934	170	18	HCIC	9	21	140	11	5	20	0
O. grisea Betten, 1934	180	5	UMMZ	0	106	74	50	0	56	0
<i>O. itascae</i> Monson & Holzenthal, 1993	4	4	HCIC	0	4	0	0	0	4	0
O. michiganensis Mosely, 1934	219	25	HCIC	120	99	0	3	32	183	1
O. novasota Ross, 1944	2	1	UMMZ	0	0	2	0	0	0	0
O. obtatus Denning, 1947	27	10	HCIC	4	15	8	12	0	5	3
O. pallida (Ross, 1904)	757	10	HCIC	0	9	748	4	1	28	0
O. rivicola Blickle & Morse, 1954	85	7	HCIC	2	83	0	1	59	25	0
O. serrata Ross, 1938	366	17	HCIC	6	319	41	315	0	11	0
O. sida Blickle & Morse, 1954	10	5	HCIC	4	6	0	0	2	8	0
O. verna Ross, 1938	3	3	HCIC	1	1	1	0	1	0	0
O. zeronia Ross, 1941	73	12	HCIC	5	26	42	25	4	5	0
Stactobiella delira (Ross, 1938)	27	4	HCIC	24	3	0	0	14	13	0
S. palmata (Ross, 1938)	14	4	HCIC	5	9	0	0	0	5	9

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
LEPIDOSTOMATIDAE (10)										
Lepidostoma bryanti (Banks, 1908)	7129	38	HCIC	157	6907	65	7	6822	300	0
L. carrolli Flint, 1958	1	1	HCIC	0	1	0	0	1	0	0
L. cinereum (Banks, 1914)	154	5	UMMZ	8	146	0	1	134	19	0
L. costale (Banks, 1914)	30	5	UMMZ	6	24	0	0	13	15	0
L. griseum (Banks, 1911)	406	8	HCIC	0	406	0	0	405	1	0
<i>L. liba</i> Ross, 1941	1	1	INHS	0	1	0	0	1	0	0
L. sackeni (Banks, 1936)	14	7	HCIC	2	12	0	0	11	3	0
L. togatum (Hagen, 1861)	5623	87	HCIC	1167	4436	2	43	1022	4417	123
L. unicolor (Banks, 1911)	4	2	HCIC	4	0	0	0	0	4	0
L. vernale (Banks, 1897)	116	10	HCIC	1	115	0	0	112	1	3
LEPTOCERIDAE (46)										
Ceraclea alagma (Ross, 1938)	1058	34	HCIC	28	867	163	841	5	52	2
C. albosticta (Hagen, 1861)	2	1	HCIC	0	2	0	2	0	0	0
<i>C. alces</i> (Ross, 1941)	1	1	HCIC	0	1	0	0	0	1	0
C. ancylus (Vorhies, 1909)	11	5	HCIC	10	0	1	1	0	9	1
C. annulicornis (Martynov, 1910)	1	1	HCIC	1	0	0	0	0	0	1
C. arielles (Denning, 1942)	3637	13	HCIC	515	3122	0	1	28	3607	1
C. cancellata (Betten, 1942)	163	31	HCIC	75	52	35	41	1	71	49
C. diluta (Hagen, 1861)	29	10	HCIC	10	8	10	22	0	5	1
C. excisa (Morton, 1904)	1	1	UMMZ	1	0	0	0	0	0	0
C. flava (Ross, 1904)	39	1	HCIC	39	0	0	0	0	0	39
C. maculata (Banks, 1899)	143	15	HCIC	39	68	36	11	1	100	31
C. mentiea (Walker, 1852)	1	1	INHS	0	0	1	0	0	0	1
C. resurgens (Walker, 1852)	7	4	HCIC	3	3	1	5	0	0	2
C. tarsipunctata (Vorhies, 1909)	1532	18	HCIC	113	1250	126	321	42	533	628
C. transversa (Hagen, 1861)	993	61	HCIC	311	666	14	53	17	866	53
C. wetzeli (Ross, 1941)	30	3	HCIC	26	4	0	0	0	4	26
Leptocerus americanus (Banks, 1899)	3037	85	HCIC	120	1010	1906	264	123	2139	365
Mystacides interjecta (Banks, 1914)	1067	52	HCIC	233	806	28	965	25	53	0
M. sepulchralis (Walker, 1852)	1774	102	HCIC	385	1299	89	1078	17	614	12
Nectopsyche albida (Walker, 1852)	2572	63	HCIC	21	2347	201	774	111	356	1278
N. candida (Hagen, 1861)	824	15	HCIC	4	92	728	90	0	350	383
N. diarina (Ross, 1944)	76	16	HCIC	9	55	12	20	2	48	1
N. exquisita (Walker, 1852)	226	19	HCIC	54	91	81	82	0	8	80
N. pavida (Hagen, 1861)	170	18	HCIC	43	125	2	90	1	77	1
Oecetis avara (Banks, 1895)	5654	37	HCIC	5321	269	69	76	2	437	5144
O. cinerascens (Hagen, 1861)	812	89	HCIC	199	465	148	494	66	144	8
O. disjuncta (Banks, 1920)	119	9	HCIC	28	90	1	0	1	116	2
O. ditissa Ross, 1966	1	1	INHS	0	1	0	1	0	0	0
<i>O. houghtoni</i> Blahnik & Holzenthal, 2014	6	2	HCIC	4	2	0	6	0	0	0
O. immobilis (Hagen, 1861)	28	8	HCIC	5	23	0	21	3	3	0
O. inconspicua (Walker, 1852)	16220	168	HCIC	1383	12262	2550	8727	2928	2184	159
O. nocturna Ross, 1966	2	2	HCIC	0	1	1	0	0	2	0
O. ochracea Curtis, 1825	3	2	INHS	1	0	2	0	0	1	0
O. osteni Milne, 1934	444	55	HCIC	71	343	30	333	16	72	17
O. persimilis (Banks, 1907)	1422	68	HCIC	365	987	70	40	222	1085	72

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
Setodes incertus (Walker, 1852)	1543	23	HCIC	905	638	0	3	13	1371	156
S. oligius (Ross, 1938)	308	16	HCIC	0	262	46	180	2	79	8
Triaenodes abus Milne, 1935	125	14	HCIC	4	15	106	8	0	10	2
T. baris Ross, 1938	57	20	HCIC	8	43	6	2	29	18	1
T. dipsius Ross, 1938	98	17	HCIC	30	68	0	3	8	87	0
T. ignitus (Walker, 1852)	186	35	HCIC	9	131	46	3	13	159	11
T. injustus (Hagen, 1861)	535	56	HCIC	152	310	68	224	69	197	4
T. marginatus Sibley, 1926	334	42	HCIC	58	197	83	2	69	188	1
T. melacus Ross, 1947	6	3	HCIC	0	0	6	4	2	0	0
<i>T. nox</i> Ross, 1941	107	26	HCIC	11	89	7	14	56	34	0
T. tardus Milne, 1934	1015	54	HCIC	58	399	557	23	165	288	5
LIMNEPHILIDAE (49)										
Anabolia bimaculata (Walker, 1852)	207	42	HCIC	72	114	10	57	21	108	1
A. consocia (Walker, 1852)	90	27	HCIC	14	64	12	3	12	61	1
A. ozburni Milne, 1935	254	5	UMMZ	0	23	231	0	0	23	0
A. sordida Hagen, 1861	9	6	INHS	1	6	2	4	0	4	0
Asynarchus montanus (Banks, 1907)	45	8	HCIC	2	15	28	3	1	12	0
A. rossi Leonard & Leonard, 1949	15	3	UMMZ	0	15	0	0	15	0	0
Frenesia missa (Milne, 1935)	159	13	UMMZ	1	156	2	1	77	77	0
Glyphopsyche irrorata (F., 1781)	7	4	HCIC	2	5	0	0	5	2	0
Hesperophylax designatus (Walker, 1852)	154	24	HCIC	17	126	11	1	119	37	0
Hydatophylax argus (Harris, 1869)	130	35	HCIC	6	119	2	1	71	54	0
Ironoquia lyrata (Ross, 1938)	4	2	HCIC	0	4	0	0	4	0	0
I. parvula (Banks, 1900)	4	2	INHS	4	0	0	2	0	2	0
I. punctatissima (Walker, 1852)	65	7	HCIC	0	26	39	0	25	0	0
Lenarchus crassus (Banks, 1920)	2	1	HCIC	2	0	0	0	1	0	0
Leptophylax gracilis Banks, 1900	11	7	UMMZ	0	6	5	0	1	0	1
Limnephilus ademus Ross, 1941	1	1	DER	1	0	0	0	0	0	0
L. argenteus Banks, 1914	1	1	HCIC	1	0	0	0	0	1	0
L. canadensis Banks, 1808	7	6	UMMZ	5	2	0	0	1	5	0
L. dispar McLachlan, 1875	6	2	UMMZ	0	0	6	0	0	0	0
L. externus Hagen, 1861	3	2	UMMZ	0	3	0	0	0	3	0
<i>L. extractus</i> Walker, 1852	1	1	INHS	1	0	0	0	0	0	0
L. hyalinus Hagen, 1861	1	1	HCIC	1	0	0	0	0	1	0
L. indivisus Walker, 1852	473	46	HCIC	2	116	351	12	65	32	6
L. infernalis (Banks, 1914)	15	5	UMMZ	14	0	0	14	0	0	0
L. janus Ross, 1938	7	1	HCIC	7	0	0	7	0	0	0
L. moestus Banks, 1908	186	44	HCIC	63	91	32	1	59	70	3
L. ornatus Banks, 1907	97	31	HCIC	33	23	41	4	15	30	1
L. parvulus (Banks, 1905)	55	3	UMMZ	3	0	52	2	0	1	0
L. perpusillus Walker, 1852	25	2	UMMZ	0	0	25	0	0	0	0
L. rhombicus (L., 1758)	62	13	HCIC	14	47	1	2	11	49	0
L. sackeni Banks, 1930	4	4	UMMZ	2	1	2	1	0	2	1
L. samoedus McLachlan, 1880	3	2	DER	0	0	0	2	0	0	0
L. secludens Banks, 1914	2	2	UMMZ	0	0	2	0	0	0	0
L. sericeus (Say, 1824)	211	16	HCIC	12	195	4	8	25	171	0
L. submonilifer Walker, 1852	529	34	HCIC	19	105	405	0	71	32	0
Nemotaulius hostilis (Hagen, 1873)	45	7	HCIC	2	43	0	0	42	2	1

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
Onocosmoecus unicolor (Banks, 1897)	73	14	HCIC	45	28	0	0	14	59	0
Phanocelia canadensis (Banks, 1924)	4	1	UMMZ	0	0	4	0	0	0	0
Platycentropus amicus (Hagen, 1861)	15	4	HCIC	4	11	0	0	0	11	4
P. radiatus (Say, 1824)	386	68	HCIC	61	230	79	64	155	79	0
P. indistinctus (Walker, 1852)	1	1	HCIC	1	0	0	0	0	1	0
Pseudostenophylax sparsus (Banks, 1908)	20	10	HCIC	7	13	0	0	11	8	0
Psychoglypha subborealis Ross, 1944	5	2	UMMZ	0	5	0	0	3	2	0
Pycnopsyche antica (Walker, 1852)	2191	12	HCIC	0	2191	0	0	2165	5	0
P. guttifera (Walker, 1852)	1387	26	HCIC	23	1348	16	9	1309	50	0
P. indiana (Ross, 1938)	13	2	HCIC	0	1	12	0	0	13	0
P. lepida (Hagen, 1861)	236	38	HCIC	85	136	11	17	92	100	0
P. scabripennis (Rambur, 1842)	4	4	INHS	0	3	1	0	3	1	0
P. subfasciata (Say, 1828)	62	11	HCIC	28	3	30	27	0	0	0
MOLANNIDAE (5)										
Molanna blenda Sibley, 1926	563	29	HCIC	48	513	2	4	513	45	1
M. flavicornis Banks, 1914	67	12	HCIC	11	0	0	10	0	1	0
M. tryphena Betten, 1934	198	42	HCIC	111	67	15	2	33	156	0
M. ulmerina Navas, 1934	22	7	INHS	2	20	0	17	0	0	5
M. uniophila Vorhies, 1909	2027	65	HCIC	105	1850	68	1915	3	80	0
ODONTOCERIDAE (1)										
Psilotreta indecisa (Walker, 1852)	1	1	UMMZ	1	0	0	0	1	0	0
PHILOPOTAMIDAE (6)										
Chimarra aterrima Hagen, 1861	549	44	HCIC	136	396	14	45	137	323	16
<i>C. feria</i> (Ross, 1941)	213	8	HCIC	0	209	4	0	210	3	0
C. obscura (Walker, 1852)	4488	62	HCIC	69	1093	3326	65	136	3773	510
C. socia (Hagen, 1861)	8744	16	HCIC	8678	68	1	2	0	93	8646
Dolophilodes distinctus (Walker, 1852)	1343	73	HCIC	297	1043	1	10	750	581	0
Wormaldia moesta (Banks, 1914)	8	3	HCIC	8	0	0	0	0	8	0
PHRYGANEIDAE (18)										
Agrypnia colorata (Hagen, 1873)	3	3	UMMZ	1	1	0	1	0	1	0
A. improba (Hagen, 1873)	147	22	HCIC	130	17	0	46	2	99	0
A. macdunnoughi (Milne, 1931)	6	3	HCIC	2	0	0	0	0	2	0
A. straminea Hagen, 1873	18	7	INHS	18	0	0	18	0	0	0
A. vestita (Walker, 1852)	49	13	HCIC	2	33	14	5	29	4	0
Banksiola crotchi Banks, 1844	2219	92	HCIC	420	1644	135	352	1094	609	19
B. dossuaria (Say, 1828)	108	7	HCIC	0	108	0	0	106	1	1
B. smithi (Banks, 1914)	73	17	HCIC	35	21	16	28	0	27	0
Beothukus complicatus (Banks, 1924)	2	2	?	2	0	0	2	0	0	0
Fabria inornata (Banks, 1907)	1	1	?	0	0	1	0	0	0	0
Hagenella canadensis (Banks, 1907)	50	10	HCIC	3	16	31	0	10	9	0
Oligostomis ocelligera (Walker, 1852)	10	1	UMMZ	0	0	0	0	0	0	0
Phryganea cinerea Walker, 1852	213	43	HCIC	101	101	2	48	62	89	4
P. sayi Milne, 1931	31	10	HCIC	0	27	4	1	24	4	0
Ptilostomis angustipennis Hagen, 1873	44	13	HCIC	1	36	7	3	33	1	0
<i>P. ocellifera</i> (Walker, 1852)	375	59	HCIC	79	252	44	42	173	126	3
P. postica (Walker, 1852)	7	6	HCIC	0	3	4	1	1	1	0
P. semifasciata (Say, 1828)	207	41	HCIC	131	48	22	14	23	161	0

Taxon	spcs	locs	Dep.	NG	NF	SA	Lk	SR	MR	LR
POLYCENTROPODIDAE (28)										
Cernotina spicata Ross, 1938	135	11	HCIC	1	70	64	64	3	4	0
Cyrnellus fraternus (Banks, 1905)	45	8	HCIC	5	2	38	15	0	6	22
Holocentropus flavus Banks, 1908	75	14	HCIC	4	18	53	3	11	12	0
H. interruptus Banks, 1914	798	47	HCIC	47	246	505	156	95	63	2
H. melanae Ross, 1938	45	8	HCIC	2	17	26	16	0	3	0
H. milaca (Etnier, 1968)	31	1	HCIC	0	31	0	31	0	0	0
H. picicornis (Stephens, 1836)	20	2	HCIC	0	0	20	0	0	0	0
Neureclipsis bimaculata (L., 1758)	42	5	HCIC	36	5	1	4	0	28	9
N. crepuscularis (Walker, 1852)	276	59	HCIC	69	174	32	17	19	197	39
N. piersoni Frazer & Harris, 1991	10	5	INHS	0	8	2	5	2	3	0
N. validus (Walker, 1852)	2	1	HCIC	2	0	0	2	0	0	0
Nyctiophylax affinis (Banks, 1897)	4982	83	HCIC	285	3496	186	3027	198	501	236
N. moestus Banks, 1911	160	17	HCIC	46	84	30	1	2	151	0
N. serratus Lago & Harris, 1985	1	1	INHS	0	1	0	1	0	0	0
Plectrocnemia albipuncta Banks, 1930	40	14	HCIC	35	5	0	3	2	35	0
P. aureola Banks, 1930	862	24	HCIC	5	2	816	4	16	26	0
P. cinerea (Hagen, 1861)	1147	81	HCIC	88	778	276	684	37	117	4
P. clinei Milne, 1936	53	17	HCIC	12	41	0	10	31	12	0
P. crassicornis (Walker, 1852)	285	14	HCIC	2	20	163	2	2	19	0
<i>P. icula</i> (Ross, 1941)	10	5	HCIC	9	1	0	0	0	10	0
P. nascotia (Ross, 1941)	28	2	HCIC	0	0	28	0	0	28	0
P. remota (Banks, 1911)	230	29	HCIC	7	51	171	4	30	25	0
P. sabulosa (Leonard & Leonard, 1949)	3	1	UMMZ	0	3	0	0	0	0	0
P. weedi (Blickle & Morse, 1955)	4	4	HCIC	0	2	2	0	1	1	0
Polycentropus centralis Banks, 1914	33	2	HCIC	33	0	0	0	0	33	0
P. confusus Hagen, 1861	27	11	HCIC	7	16	0	0	0	21	1
P. pentus Ross, 1941	678	63	HCIC	101	541	36	8	354	296	13
P. timesis (Denning, 1948)	15	4	HCIC	0	15	0	0	15	0	0
PSYCHOMYIIDAE (2)										
Lype diversa (Banks, 1914)	1589	94	HCIC	391	1101	97	12	449	1101	27
Psychomyia flavida Hagen, 1861	10574	127	HCIC	4291	6070	207	248	1102	6402	2644
RHYACOPHILIDAE (8)										
Rhyacophila brunnea Banks, 1911	78	9	HCIC	28	50	0	0	44	19	0
<i>R. fuscula</i> (Walker, 1852)	42	14	HCIC	421	1	0	0	0	366	56
R. glaberrima Ulmer, 1907	1	1	INHS	0	1	0	0	0	1	0
R. ledra Ross, 1939	1	1	HCIC	0	0	1	0	0	1	0
R. lobifera Betten, 1834	5	1	HCIC	0	0	5	0	0	0	5
R. mainensis Banks, 1911	29	6	HCIC	3	26	0	0	4	24	1
R. manistee Ross, 1939	313	15	HCIC	0	313	0	0	32	244	37
R. vibox Milne, 1936	246	12	HCIC	11	233	0	1	236	7	0
SERICOSTOMATIDAE (1)										
Agarodes distinctus (Ulmer, 1905)	125	9	HCIC	6	18	101	16	0	5	3
THREMMATIDAE (3)										
Neophylax concinnus McLachlan, 1871	185	32	HCIC	86	92	7	11	45	127	1
N. fuscus Banks, 1903	54	4	UMMZ	0	54	0	0	0	54	0
N. oligius Ross, 1938	134	18	HCIC	19	80	35	0	62	58	4

Species	Explanation
Banksiola selina Betten, 1944	Junior synonym of B. crotchi (Wiggins 1956)
Ceraclea nepha (Ross, 1944)	Reported from "Crawford". No specimen located
Ceraclea punctata (Banks, 1894)	Reported from "Crawford". No specimen located
Cyrnellus marginalis (Banks, 1930)	Junior synonym of C. fraternus (Flint 1964)
Dicosmoecus quadrinotatus (Banks, 1908)	Junior synonym of <i>Onocosmoecus unicolor</i> (Wiggins and Richardson 1986)
Hydropsyche alvata Denning, 1949	Junior synonym of H. incommoda (Korecki 2006)
Hydropsyche bidens Ross, 1938	Junior synonym of H. incommoda (Korecki 2006)
Hydropsyche bifida Banks, 1905	Junior synonym of H. morosa (Schefter and Unzicker 1984)
Hydropsyche orris Ross, 1938	Junior synonym of H. incommoda (Korecki 2006)
Hydropsyche recurvata Banks, 1908	Junior synonym of <i>H. alternans</i> (Schefter and Wiggins 1986)
Holocentropus glacialis Ross, 1938	Misidentified. Is Plectrocnemia cinerea (INHS)
Lepidostoma strophis Ross, 1938	Junior synonym of L. cinereum (Weaver 1988)
Neophylax autumnus Vorhies, 1909	Junior synonym of N. concinnus (Kimmins and Denning 1951)
Nyctiophylax uncus Ross, 1944	Misidentified. Is N. affinis (INHS)
Nyctiophylax vestitus (Hagen, 1861)	Nomen dubium (Morse 1972)
Platycentropus plectrus Ross, 1938	Junior synonym of P. amicus (Flint 1966)
Rhyacophila acropedes Banks, 1914	Junior synonym of R. brunnea (Smith 1984)
Rhyacophila melita Ross, 1938	Junior synonym of <i>R. mainensis</i> (Smith 1984)

Table 3. Species from Leonard and Leonard's (1949b) checklist that are considered doubtful due to synonymy, misidentification, or our inability to locate a specimen.



Species ranked in descending order of abundance

Figure 2. The number of specimens known for each Michigan species and the number of localities where each species has been found.



Figure 3. The number of total and unique species from Michigan habitat types (**A**) and caddisfly regions (Houghton 2015) (**B**).

Rhyacophila lobifera Betten (Rhyacophilidae), whose presence in Michigan is based on larvae and genetic analysis (Abigail Fusaro, unpublished data). Adult male specimens of *Beothukus complicatus* (Banks) (Phryganeidae) were collected by PLH and identified by BJA. The specimens were subsequently lost. Due to the distinctness of the male genitalia, it is unlikely that these specimens were misidentified and so *B. complicatus* is included on the checklist. Likewise, *Fabria inornata* Banks (Phryganeidae) was included in Leonard and Leonard's (1949b) checklist. We have not been able to locate specimens, but find it unlikely that this distinctive species was misidentified and so have included it on the checklist. Conversely, *Ceraclea nepha* (Ross) and *C. punctata* (Banks) are more difficult to identify so, in the absence of known specimens, are excluded from the checklist (Table 3).



Figure 4. The number of species within families found in Ohio (Armitage et al. 2011), Michigan (present study), and Minnesota (Houghton 2012).

Michigan caddisfly species richness appears similar to that of Minnesota (277 total species) and Ohio (272), two adjacent states where surveys of comparable effort have recently occurred (Armitage et al. 2011, Houghton 2012). All three states generally harbor similar numbers of species in the same families; exceptions include Brachycentridae, Glossosomatidae, Hydropsychidae, Limnephilidae, Phryganeidae, and Rhyacophilidae (Figure 4). Overall distribution of specimens per species (Figure 2) follows a similar pattern in both states (Houghton and Holzenthal 2010).

Michigan and Minnesota also exhibit similar regional patterns, with higher species richness in the Northern Great Lakes and Northern Forested regions than in the Southern Agricultural region (Houghton 2012). These differences are probably due to both natural and anthropogenic factors (Houghton 2015). The majority of streams of the Northern Great Lakes region drain into Lake Superior and are of high gradient, especially their downstream sections. The majority of the region is forested, leading to low levels of watershed disturbance. The Northern Forested region is also relatively undisturbed. Most streams drain into lakes Michigan and Huron and tend to be of lower gradient. Streams of the Southern Agricultural region also tend to be low gradient. The region contains >90% of Michigan's human population (www.census.gov) and most of its agriculture. Thus, streams are surrounded by anthropogenic disturbance.

Although the majority of Michigan caddisflies have also been collected from adjacent states and provinces, and Michigan does not have any known endemic species, there are still some noteworthy Michigan records reported in this study. Polycentropus timesis (Denning) (Polycentropodidae) is known in Michigan from 4 sites in Lake County in the northwestern Lower Peninsula. These sites are separated by >800 km from the other known P. timesis collection sites in Massachusetts and New Hampshire (Weaver 1995). Prior to the Michigan collections, Holocentropus milaca (Etnier) (Polycentropodidae) and Oxyethira itascae Monson and Holzenthal (Hydroptilidae) were both thought to be endemic to Minnesota (Houghton and Holzenthal 2003). Hydroptila tusculum Ross (Hydroptilidae) was previously known only from collections in the southeastern U.S. (Moulton and Stewart 1996); the nearest reported collection is ~1,200 km from the single Michigan locality in the northwestern Lower Peninsula. Interestingly, *H. tusculum* has also been collected from Wisconsin (unpublished data), indicating that it is more widespread than originally thought. Similarly, Neureclipsis piersoni Frazer and Harris and Nyctiophylax serratus Lago and Harris (Polycentropodidae) are known in Michigan from Sleeping Bear Dunes National Park in the northwestern Lower Peninsula. Both species represent >500 km range extensions from their nearest known collecting localities in Kentucky (Rasmussen and Morse 2016).

Including the current study, 20% of the total caddisfly fauna of Michigan, and almost 40% of the hydroptilid fauna, has been reported during the last 10 years, despite a >80-year collecting history in the state (Table 1). Moreover, nearly all recent regional studies have resulted in new state records. Thus, it is likely that additional species remain undiscovered in the state. Future research will include a more comprehensive faunal analysis relating species to habitat preferences and anthropogenic disturbance levels, as well as a conservation assessment of individual Michigan species.

Acknowledgments

We appreciate the efforts of all who have collected, sorted, and identified Michigan caddisflies, including Benjamin Albers, Doug Bidlack, Roger Blahnik, Chris Bowyer, Kelsey Brakel, Kiralyn Brakel, the Friends of the Rogue River, Erin Furmaga, Abi-gail Fusaro, Hannah (Russell) Goble, Bruce McCulloch, Bilyana (Petkova) McLeod, Bridget O'Leary, Joel Parker, Sally Petrella, Logan Shoup, Mary Clare Smith, Erich Steger, Peter Thistleton, Eleanor (Smith) Valle, Jeff Van Zant, Lydia Wassink, and Daniel Wright. We further thank Abigail Fusaro and the Friends of the Rogue River for sharing larval specimens and genetic sequence data for *Rhyacophila lobifera*. We thank Mark O'Brien (University of Michigan), Ralph Holzenthal (University of Minnesota), Richard Baumann (Brigham Young University), and Boris Kondratieff (Colorado State University) for allowing us access to additional records and collections.

Permit PRD-SU-2011-039 to collect from Michigan State Park habitats was provided by Alicia Selden of the Michigan Department of Natural Resources. Sampling of Sleeping Bear Dunes National Park was conducted under permit SLBE-2014-SCI-0002, facilitated by Kevin Skerl, Chief of Natural Resources for the park. Permission to sample in the Huron Mountains was provided by the Huron Mountains Wildlife Federation. Permission to sample at the Black River Ranch was provided by the Black River Ranch Board of Directors. Permission to sample at Sarah Jane's Natural Area was provided by John Bagley and Andrew Bacon of the Michigan Nature Association.

Research costs were supported by the Hillsdale College biology department and several LAUREATES grants from Hillsdale College to DCH, AJP, and affiliated students. RED received support from the US Department of Interior (INT RD X-1-R-1) and the National Science Foundation (DEB 09-18805 ARRA). The valuable comments of Ralph Holzenthal, Karl Kjer, and Andy Rasmussen improved earlier versions of the manuscript. This is paper #17 of the G.H. Gordon BioStation Research Series.

References

- Armitage BJ, Harris SC, Schuster GA, Usis JD, MacLean DB, Foote BA, Bolton MJ, Garono RJ (2011) Atlas of Ohio aquatic insects, Volume 1: Trichoptera. Ohio Biological Survey Miscellaneous Contributions, 13.
- Barbour MT, Gerritsen J, Snyder BD, Stribling JB (1999) Rapid bioassessment protocols for use in streams and wadeable Rivers: periphyton, benthic macroinvertebrates and fish, 2nd ed. EPA 841-B-99-002. U. S. Environmental Protections Agency, Office of Water. Washington, DC.
- Bright E (2017) Aquatic insects of Michigan. http://www.aquaticinsects.org/sp/Trichoptera/ sp_tom.html [Accessed 18 October 2017]
- Colwell RK (2007) Biota II: The biodiversity database manager. Sinauer Associates, Ltd., Sunderland, Massachusetts.
- Davis BM, Hudson PL, Armitage BJ (1991) Distribution and abundance of caddisflies (Trichoptera) in the St. Clair-Detroit river system. Journal of Great Lakes Research 17: 522–535. https://doi.org/10.1016/S0380-1330(91)71388-9
- DeWalt RE, South EJ (2015) Ephemeroptera, Plecoptera, and Trichoptera in Isle Royale National Park, USA, compared to mainland species pool and size distribution. Zookeys 532: 137–158. https://doi.org/10.3897/zookeys.532.6478
- Ellis RJ (1962) Adult caddisflies (Trichoptera) from Houghton Creek, Ogemaw County, Michigan. Occasional papers of the Museum of Zoology, University of Michigan 624: 1–16.
- Flannagan PM, Flannagan JF (1982) Present distribution and the post-glacial origin of the Ephemeroptera, Plecoptera, and Trichoptera of Manitoba. Manitoba Department of Natural Resources Technical Report 82: 1–79.
- Flint Jr. OS (1964) Notes on some Nearctic Psychomyiidae with special reference to their larvae (Trichoptera). Proceedings of the United States National Museum 115: 467–481. https:// doi.org/10.5479/si.00963801.115-3491.467
- Flint Jr. OS (1966) Notes on certain Nearctic Trichoptera in the Museum of Comparative Zoology. Proceedings of the United States National Museum 118: 373–390. https://doi. org/10.5479/si.00963801.118-3530.373
- Harris SC, Lago PK, Carlson RB (1980) Preliminary survey of the Trichoptera of North Dakota. Proceedings of the Entomological Society of Washington 82: 39–43.
- Houghton DC (2012) Biological diversity of Minnesota caddisflies. ZooKeys Special Issues 189: 1–389. https://doi.org/10.3897/zookeys.189.2043
- Houghton DC (2015) Delineation and characterization of the Michigan, USA, caddisflies (Insecta: Trichoptera) and comparison with Minnesota. Journal of Freshwater Ecology 30: 525–542. https://doi.org/10.1080/02705060.2014.1002544
- Houghton DC (2016) The caddisflies (Trichoptera) of an undisturbed Lower Michigan habitat. The Great Lakes Entomologist 49: 41–54.
- Houghton DC, Holzenthal RW (2003) Updated conservation status of protected Minnesota caddisflies (Trichoptera). The Great Lakes Entomologist 36: 35–40.
- Houghton DC, Holzenthal RW (2010) Historical and contemporary biological diversity of Minnesota caddisflies: a case study of landscape-level species loss and trophic composition shift. Journal of the North American Benthological Society 29: 480–495. https://doi. org/10.1899/09-029.1
- Houghton DC, Brandin CM, Brakel KA (2011) Analysis of the caddisflies (Trichoptera) of the Manistee River watershed, Michigan. Great Lakes Entomologist 44: 1–15.
- Kimmins DE, Denning DG (1951) The McLachlan Types of North American Trichoptera in the British Museum. Annals of the Entomological Society of America 44: 111–140. https://doi.org/10.1093/aesa/44.1.111
- Korecki JA (2006) Revision of the males of the *Hydropsyche scalaris* group in North America (Trichoptera: Hydropsychidae). MS thesis, Clemson University, Clemson, SC. ProQuest Dissertations Publishing, 1439244.
- Leonard JW, Leonard FA (1949a) Noteworthy records of caddis flies from Michigan, with descriptions of new species. Occasional papers of the Museum of Zoology, University of Michigan 520: 1–8.
- Leonard JW, Leonard FA (1949b) An annotated list of Michigan Trichoptera. Occasional papers of the Museum of Zoology, University of Michigan 522: 1–35.
- Longridge JW, Hilsenhoff WL (1973) Annotated list of the Trichoptera (caddisflies) in Wisconsin. Wisconsin Academy of Science, Arts, and Letters 61: 241–256.
- Morse JC (1972) The genus Nyctiophylax in North America. Journal of the Kansas Entomological Society 45: 172-181.
- Morse JC (Ed.) (2017) Trichoptera World Checklist. http://entweb.clemson.edu/database/ trichopt/index.htm [Accessed 18 October 2017]
- Moulton SR, Stewart KW (1996) Caddisflies (Trichoptera) of the interior highlands of North America. Memoirs of the American Entomological Institute 56: 1–313.
- Rasmussen AK, Morse JC (2016) Distributional Checklist of Nearctic Trichoptera (Summer 2016 Revision). Unpublished, Florida A&M University, Tallahassee, 498 pp. http://www. Trichoptera.org
- Ross HH (1938) Descriptions of Nearctic caddis flies (Trichoptera) with special reference to the Illinois species. Bulletin of the Illinois Natural History Survey 21: 101–83.
- Ross HH (1941) Descriptions and records of North American Trichoptera. Transactions of the American Entomological Society 67: 35–126.

- Ross HH (1944) The caddis flies or Trichoptera of Illinois. Bulletin of the Illinois Natural History Survey 23: 1–326.
- Ross HH (1946) A review of Nearctic Lepidostomatidae (Trichoptera). Annals of the Entomological Society of America 39: 265–91. https://doi.org/10.1093/aesa/39.2.265
- Schefter PW, Unzicker JD (1984) A review of the *Hydropsyche morosa-bifida* complex in North America (Trichoptera: Hydropsychidae). Proceedings of the 4th International Symposium on Trichoptera. Junk, The Hague, 331–35.
- Schefter PW, Wiggins GB (1986) A systematic study of the Nearctic larvae of the Hydropsyche morosa Group (Trichoptera: Hydropsychidae). Royal Ontario Museum Life Science Miscellaneous Publications, 94 pp. https://doi.org/10.5962/bhl.title.60680
- Smith SD (1984) Larvae of Nearctic *Rhyacophila*, part 1: *acropedes* group. Aquatic Insects 6: 37–40. https://doi.org/10.1080/01650428409361159
- Waltz RD, McCafferty WP (1983) The caddisflies of Indiana. Agricultural Experimental Station Bulletin 978, Purdue University, Lafayette, IN.
- Weaver JS III (1988) A synopsis of the North American Lepidostomatidae (Trichoptera). Contributions of the American Entomological Institute 24: 1–141.
- Weaver JS III (1995) Transfer of *Neureclipsis timesis* Denning to *Polycentropus*. Proceedings of the Entomological Society of Washington 97: 892.
- Wiggins GB (1956) A revision of the North American caddisfly genus *Banksiola* (Trichoptera: Phryganeidae). Contributions of the Royal Ontario Museum, Division of Zoology and Paleontology 43: 1–12. https://doi.org/10.5962/bhl.title.52191
- Wiggins GB, Richardson JS (1986) Revision of the Onocosmoecus unicolor group. Psyche 93: 187–216. https://doi.org/10.1155/1986/82592

Supplementary material I

Data file for new state records

Authors: David C. Houghton, R. Edward DeWalt, Angelica J. Pytel, Constance M. Brandin, Sarah E. Rogers, David E. Ruiter, Ethan Bright, Patrick L. Hudson, Brian J. Armitage

Data type: speciemens data

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.730.21776.suppl1

RESEARCH ARTICLE



A new lineage of braconid wasps in Burmese Cenomanian amber (Hymenoptera, Braconidae)

Michael S. Engel^{1,2,3}, Diying Huang⁴, Chenyang Cai⁴, Abdulaziz S. Alqarni⁵

I Division of Entomology, Natural History Museum, University of Kansas, 1501 Crestline Drive – Suite 140, Lawrence, Kansas 66045-4415, USA 2 Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA 3 Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA 4 State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China 5 Department of Plant Protection, College of Food and Agriculture Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Kingdom of Saudi Arabia

Corresponding author: Michael S. Engel (msengel@ku.edu)

Academic editor: C. van Achterberg Received 28 November 2017 Accepted 10 January 2018 Published 17 January 2	2018
http://zoobank.org/62307871-22BB-458B-9DB6-B161A3418DCF	

Citation: Engel MS, Huang D, Cai C, Alqarni AS (2018) A new lineage of braconid wasps in Burmese Cenomanian amber (Hymenoptera, Braconidae). ZooKeys 730: 75–86. https://doi.org/10.3897/zookeys.730.22585

Abstract

A new braconid wasp from the Upper Cretaceous (Cenomanian) amber of the Hukawng Valley in Kachin State, Myanmar is described and figured from a unique female. *Seneciobracon novalatus* Engel & Huang, **gen. et sp. n.**, is placed in a distinct subfamily, Seneciobraconinae Engel & Huang, **subfam. n.**, owing to the presence of a unique combination of primitive protorhyssaline-like traits, with an otherwise more derived wing venation. The fossil is discussed in the context of other Cretaceous Braconidae.

Keywords

Cretaceous, Euhymenoptera, fossil, Ichneumonoidea, Myanmar, parasitoid, taxonomy, wasp

Introduction

Although braconids are a frequently encountered lineage in the modern hymenopteran fauna (Grimaldi and Engel 2005; Quicke 2015), and are represented in Cenozoic ambers by diverse subfamilies (e.g., Brues 1933, 1939; van Achterberg 1982, 2001; Tobias 1987; Zuparko and Poinar 1997; Engel and Bennett 2008; Butcher et al. 2014), their

presence in fossiliferous resins from the Cretaceous is comparatively scant. This diverse clade of parasitoid wasps is today represented by over 21,200 described species (Aguiar et al. 2013; Yu et al. 2016), and with an actual diversity of perhaps more than double what is already known (Quicke 2015). Based on current estimates of relationships among the subfamilies (Sharanowski et al. 2011) and coupled with the breadth of these same groups represented in Lower Cenozoic deposits, it is clear that much of the cladogenesis among the higher groups within the family had already transpired, with these lineages extending well into the Cretaceous. It is therefore surprising that so few braconids have been recovered from Cretaceous deposits, and although several interesting new taxa have been described recently, they remain relatively rare with hitherto only 11 formally named species (*vide* Discussion, *infra*). Nonetheless, those that have been documented are interestingly phylogenetically basal to crown-group Braconidae (e.g., Perrichot et al. 2009), and so have the greatest potential for illuminating our understanding of the phases of braconid diversification.

Here we describe a new genus and species of braconid wasps in Burmese amber (Fig. 1A). The genus is interesting in that it intermixes primitive and derived features in a unique combination not attributable to any of the recognized subfamilies, and is therefore placed within a new, extinct subfamilial lineage putatively more closely related to modern cyclostome braconids than the basal Eoichneumoninae and Protorhyssalinae. The subfamily is similar to modern Rhyssalini, sharing varied plesiomorphies with this group, but can be distinguished in features of the notal and metasomal structure as well as wing venation and putatively apomorphic effacement of the occipital carina.

Material and methods

A small flake of Upper Cretaceous amber from Myanmar was discovered to contain a tiny braconid wasp, which is here designated as the holotype for the species described. The chip of amber is 8.9 mm at its maximum length, 5.4 mm in maximum width, and approximately 1.7 mm deep. While flat surfaces could be polished on the larger planes, permitting lateral views of the specimen, the narrow edges are rough and could not be cleaned further owing to the close proximity of the wasp's anterior end near one border (Fig. 1A). Overall, however, the wasp is in exceptional condition, with the antennae extended upward and curving back toward the body, the legs either extended or folded beneath the body, and the ovipositor extended. The wings extend above the body and although their apical quarters are slightly bent (each wing bending slightly to the animal's left, and therefore into the background in figure 1A), the venation can be seen beautifully. The only challenging details to discern are those of the metasoma, where much is hidden by small lateral fractures along the body, and a darkening of the amber near the body. The same holds for portions of the mesosoma, but is not as impactful on observations for this tagma.

We document the present fossil in the interest of elaborating character combinations of Cretaceous Braconidae and in the hopes that these will ultimately aid our resolution of basal relationships among lineages of braconids, with descriptive work such as this forming the basis for such discovery (sensu Grimaldi and Engel 2007). For the morphological account we have used an amalgamation of the morphological terminologies proposed by Huber and Sharkey (1993), van Achterberg (1993), and Sharkey and Wharton (1997), the latter two specific to Braconidae. Photographs of the holotype were taken through an Infinity K-2 long-distance microscope lens, using a Canon 7D digital camera, while line drawings were made with the aid of camera lucida attached to an Olympus SZX-12 stereomicroscope. The specimen was measured using the same stereomicroscope and done with the aid of an ocular micrometer. The amber locality has been mapped by Cruickshank and Ko (2003) and Grimaldi and Ross (2017), who also provide a geological account of the deposits. The amber has been dated to the earliest Cenomanian (approximately 98.8 Ma) (Shi et al. 2012).

Systematic paleontology

Family Braconidae Nees von Esenbeck

Seneciobraconinae Engel & Huang, subfam. n.

http://zoobank.org/152DB385-88D6-441C-B480-9D824396FF8D

Type genus. Seneciobracon Engel and Huang, gen. n.

Diagnosis. Head orthognathous, cyclostome; clypeus shorter than wide, protruding; hypoclypeal depression deep (Fig. 2A); mandibles short, about as long as compound eye width; antenna filiform, with 19 flagellomeres; flagellum with sparse multiporous plate sensilla; occipital carina present but incomplete, present and strong only near mandible, otherwise effaced; compound eyes without ocular setae. Pronotal collar distinct; notauli deeply impressed, percurrent, simple, not meeting posteromedially; mesoscutal lateral areas swollen, smooth; mesoscutellum slightly raised relative to surface of mesoscutum; epicnemial carina present; postpectal carina absent; precoxal sulcus absent. Forewing (Figs 1A, 2B) with short, narrow costal cell, otherwise C+Sc+R fused along length; 1Rs exceedingly short, forming straight line with 1M; rs-m present, nebulous (i.e., two closed submarginal cells); 1m-cu meeting first submarginal cell (thus Rs+M divided into long 1Rs+M and short 2Rs+M); 2m-cu absent; 1cu-a postfurcal; 2cu-a absent; stubs of 1a and 2a absent. Hind wing (Fig. 2C) with sc+r-m lacking bulla, much shorter than 1M; m-cu absent; bulla present between 1A and apex of 1Cu; 2Cu absent. Metasomal tergum I apparently without dorsope; ovipositor elongate but slightly shorter than metasoma.

Seneciobracon Engel & Huang, gen. n.

http://zoobank.org/F589489E-A107-4161-A188-A3A19151ADAA

Type species. Seneciobracon novalatus Engel & Huang, sp. n.

Diagnosis. As for the subfamily (vide supra).

Etymology. The new generic name is a combination of the Latin *senecio*, meaning, "old man", and *Bracon* Fabricius, type genus of the family. The gender of the name is masculine.

Seneciobracon novalatus Engel & Huang, sp. n.

http://zoobank.org/4B94ADA2-48F7-4EB2-B3FE-DE4DEBD141DA Figs 1–2

Holotype. \bigcirc (Fig. 1A), NIGP 164784, lowermost Cenomanian (near Albian boundary), Hukawng Valley, Kachin State, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Diagnosis. As for the subfamily (*vide supra*).

Description. \bigcirc : Total length 2.0 mm (as preserved, excluding ovipositor); forewing length 1.50 mm, hind wing length 1.35 mm; integument dark brown (Fig. 1A), lighter on mouthparts, tarsi, ovipositor, and ovipositor sheaths; wing veins brown to dark brown, membranes hyaline.

Head apparently longer than broad (direct facial view not possible, observable in frontal-oblique view: Fig. 2a), impunctate and imbricate, with sparse, minute setae on face, such setae slightly longer on clypeus; face below antennal toruli faintly convex, sloping to distinct impression along epistomal sulcus; clypeus protruding, rounded, short, medial length about one-third that of length of face from antennal toruli to epistomal sulcus; hypoclypeal depression deep and wide; mandible short, just meeting opposing mandible when closed, apparently with a single, minute, subapical tooth; maxillary palpus elongate, longer than head, with 6 palpomeres, with palpomeres II-VI longer than wide, individual palpomeres with dense, minute setae; compound eye large and glabrous, length 0.28 mm, much broader than gena, inner margin not emarginate; ocelli positioned on top of vertex; ocelli well separated, median ocellus separated from lateral ocelli by approximately twice median ocellar diameter, lateral ocelli separated from posterior of head by almost twice median ocellar diameter, ocellocular distance slightly more than twice ocellar diameter; antenna slightly shorter than body length (excluding ovipositor); scape twice as long as apical width, length 0.08 mm, width 0.04 mm, truncate apically; pedicel about 1.75 times as long as wide, about as broad as scape, length 0.07 mm; flagellum with 19 flagellomeres; basal flagellomeres elongate and of approximately equivalent widths, flagellomere I length 0.15 mm, width 0.03 mm; flagellomere II length 0.12 mm; flagellomere III length 0.12 mm; remaining flagellomeres progressively tapering in length toward apex, apical flagellomeres about 2.0–2.25 times as long as wide except apicalmost flagellomere slightly more than 3 times as long as wide; multiporous plate sensilla sparse; apicalmost flagellomeres with a short, thick, peg-like seta at apex.

Mesosoma length 0.75 mm; pronotal collar distinct; pronotal surface smooth, dorsope and laterope absent; mesoscutum smooth, raised above pronotum; notauli deeply



Figure 1. Photographs of holotype female (NIGP 164784) of *Seneciobracon novalatus* Engel & Huang, gen. et sp. n., in mid-Cretaceous amber from northern Myanmar. **A** Holotype in right lateral view as preserved **B** Inset detail of pterostigmal region of forewing, depicting small costal cell.

impressed, simple, percurrent but not meeting; lateral areas of mesoscutum (lateral to notauli) distinctly raised, convex; mesoscutellar sulcus deeply impressed, simple; mesoscutellum slightly raised, convex, smooth; mesopleuron smooth; propodeum areolate. Legs slender, with numerous setae; metafemur swollen; tibial spurs short, protibial calcar slightly curved, without comb; tibiae without spines or peg-like setae; metatibia length 0.63 mm; basitarsi largest tarsomeres, but shorter than combined length of remaining tarsomeres; pretarsal claws short, simple; arolium small. Forewing (Fig. 2B) with minute costal cell present apically near base with pterostigma, otherwise C+Sc+R fused along length; pterostigma large, longer than wide, with border inside marginal cell comparatively straight, anterior border convex, bulging; marginal cell large, extending nearly to wing apex, broad, broader than pterostigmal width; 1Rs exceedingly short, forming straight line with 1M; 1Rs+M originating near prestigma; 1M straight; 1Rs+M long, slightly curved, extending strongly posteriad to meet 1mcu; 1m-cu meeting Rs+M near longitudinal tangent of M+Cu; 2Rs+M present, exceedingly short; first submarginal cell trapezoidal, but nearly triangular owing to short 2Rs+M; second submarginal cell large, nearly square, apical border formed of nebulous rs-m; r-rs arising slightly distad pterostigmal midlength, much shorter than 3Rs, at least 2 times longer than 1Rs; 1cu-a postfurcal; 1Cu shorter than 1cu-a; 2Cu much longer than 1Cu; 2cu-a absent, thus subdiscal cell open; stubs of 1a and 2a absent. Hind wing (Fig. 2C) with margins setose and secondary 'hamuli' (two distinctively elongate setae on anterior margin at apex of C); 3 distal hamuli present on R; R tubular on anterior wing margin for short distance, otherwise extending as nebulous vein to near wing apex; 2Sc+R distinct, longer than sc+r-m; sc+r-m without bulla; Rs tubular



Figure 2. Head and wing venation of *Seneciobracon novalatus* Engel & Huang, gen. et sp. n., in Burmese amber. A Head in left lateral view **B** Forewing. **C** Hind wing.

near base then extending as nebulous vein; 2M tubular near base then nebulous; 1Cu shorter than 1M; 2Cu absent; bulla present between apex of A and Cu.

Metasoma length 1.0 mm; terga with integument transversely wrinkled, otherwise impunctate, with sparse, minute setae; sterna apparently smooth and impunctate; tergum I about as long as wide, terga II and III apparently longer than wide, fused; remaining terga transverse; dorsope of tergum I apparently absent; ovipositor long, straight, shorter than metasoma when exerted, length 0.80 mm; ovipositor sheaths slightly broader apically, with abundant minute setae.

 $\mathcal{E}: Latet.$

Etymology. The specific epithet is a combination of the Latin *novus*, meaning, "new", and *alatus*, meaning, "wing", and is a reference to the more derived wing venation relative to other Cretaceous amber Braconidae (e.g., the protorhyssalines and *Aenigmabracon* Perrichot et al.).

Discussion

The new subfamily is most similar to the modern, putatively primitive Rhyssalinae, and the tribe Rhyssalini in particular (van Achterberg 1993; Belokobylskij 2009), and

both subfamilies are rather generalized cyclostomes. Seneciobracon novalatus has a distinctive combination of traits not found among rhyssalines such as the absence of the stub of 2a in the forewing, complete absence of m-cu in the hind wing (even as a spectral trace), presence of a well-defined 2Rs+M (1m-cu typically confluent with 2Rs in Rhyssalini), presence of a distinct costal cell at the apex of the otherwise fused C+Sc+R, incomplete occipital carina (present only near mandibles), and absence of a dorsope on metasomal tergum I. Both Seneciobraconinae and Rhyssalinae, although cyclostome, differ from the extinct Protorhyssalinae in the absence of hind wing 2Cu, a putatively derived feature as 2Cu is present in Eoichneumoninae, Protorhyssalinae, Trachypetinae, Apozyginae, and Ichneumonidae. In addition, both lack the five-sided second submarginal cell more typical of the protorhyssalines (e.g., Basibuyuk et al. 1999; Perrichot et al. 2009; Ortega-Blanco et al. 2011; Engel 2016; Engel and Wang 2016; Engel et al. 2017), a condition that results from the meeting of 1m-cu with the second submarginal cell. In this regard, Seneciobracon novalatus has a venation that is more similar to modern Braconidae than to any of the other mid-Cretaceous or older braconids, and cannot be included within Protorhyssalinae or the more basal stem of Braconidae (sensu Perrichot et al. 2009). The subfamily Seneciobraconinae could be interpreted as a basal tribe in a more broadly circumscribed Rhyssalinae, although the list of differences from traditional rhyssalines listed above warrants against such inclusion at this time. Accordingly, we have preferred to recognize the former as distinct pending definitive cladistic evidence for such a clade and particularly given the challenges in defining a definitively monophyletic Rhyssalinae and the composition and circumscription of the subfamily remains somewhat in flux, albeit improving (Quicke 2015). Moreover, the putatively apomorphic dorsal effacement of the occipital carina tends to further support the subfamily. A similarly derived trait is found in Histeromerus Wesmael (formerly as Histeromerinae), a derived rhyssaline also lacking a complete occipital carina (e.g., Sharanowski et al. 2011), but otherwise differing from the fossil described herein (e.g., van Achterberg 1984, 1992).

Quicke (2015, p. 210) questioned whether the short, narrow costal cell present apically in some Cretaceous fossil Braconidae might be an artefact of preservation. It is clear that this is not the case, as evidenced nicely in the present fossil (Fig. 1B). The same condition is present in most of the known protorhyssalines (Perrichot et al. 2009; Engel 2016; Engel and Wang 2016; Engel et al. 2017), as well as *Aenigmabracon* (Perrichot et al. 2009). This character-state appears to be a primitive feature among Cretaceous braconids.

Aside from *S. novalatus*, there have hitherto been 11 Cretaceous amber Braconidae described – *Archephedrus stolamissus* Ortega-Blanco et al. and *Protorhyssalopsis perrichoti* Ortega-Blanco et al. in Albian Spanish amber; *Archaeorhyssalus subsolanus* Engel and *Rhetinorhyssalus morticinus* Engel in Cenomanian Burmese amber, *Protorhyssalodes arnaudi* Perrichot et al. and *Aenigmabracon capdoliensis* Perrichot et al. in Cenomanian amber from France; *Protorhyssalus goldmani* Basibuyuk et al. and *Rhetinorhyssalus allani* (Brues), '*Pygostylus' patriarchicus* Brues, and '*Neoblacus' facialis* Brues in Campanian

amber from Canada (Brues 1937; Basibuyuk et al. 1999; Perrichot et al. 2009; Ortega-Blanco et al. 2009, 2011; Engel 2016; Engel and Wang 2016; Engel et al. 2017). Given their prodigious modern diversity, this representation from the Cretaceous is disappointing. Ichneumonoidea generally are uncommon in Cretaceous amber, with comparatively few species described to date. As noted by McKellar and Engel (2012) and McKellar et al. (2013a), this dearth of material is perhaps the result of a bias toward the capture of often smaller-bodied animals in amber, while modern ichneumonoids include many groups of larger sizes, particularly among Ichneumonidae, as well as smaller wasps. However, where known, most Cretaceous ichneumonoids are on the smaller end of the size spectrum, including those preserved as compressions (e.g., Townes 1973; Zhang and Rasnitsyn 2003; Kopylov 2011, 2012; Belokobylskij 2012), and one might speculate that large-sized species simply did not exist during the period. However, given that the majority of wasps known from Cretaceous amber are often of smaller proportions (i.e., 12 mm or less) (e.g., Liu et al. 2007; Engel and Grimaldi 2009; McKellar and Engel 2012; Engel et al. 2013, 2017), and this is also true for coeval ants (e.g., Engel and Grimaldi 2005; McKellar et al. 2013b, 2013c; Barden and Grimaldi 2013, 2014, 2016; Perrichot et al. 2016; Barden et al. 2017), one might conclude that the taphonomic bias is true. This is particularly evident when one considers that larger arthropod inclusions are certainly well known, with numerous such examples in these same resins (e.g., Grimaldi et al. 2002; Engel and Grimaldi 2008), and certainly this is the case in the diverse Cenozoic ambers (e.g., Engel 1995, 2014; Engel and Grimaldi 2007). Thus, the result of such a taphonomic bias would be that there are any number of 'ghost' lineages and for which there assuredly should have been representatives in the Cenomanian (e.g., larger ichneumonoids, varied sizeable aculeates [such as scoliids], siricoid wood wasps, &c.). However, given the adept flight of many Hymenoptera, a large-bodied wasp would have a better chance of avoiding contact with the flowing resin and, should it become entangled, would then have a similarly greater probability of freeing itself without damage. While this would certainly minimize the presence of Ichneumonidae, most of the primitive lineages of Braconidae are quite small, such as Rhyssalinae (Quicke 2015), and so should be more readily represented in amber. It is therefore quite vexing that braconids are, in fact, so rare in Cretaceous amber.

Parasitoid wasps of the family Braconidae remain a rarity in Cretaceous amber, despite the growing number of deposits with abundant arthropod inclusions (e.g., Azar et al. 2010; Perrichot and Néraudeau 2014; Grimaldi and Ross 2017). Nonetheless, the few species known, including *Seneciobracon novalatus* described herein, reveal a fauna largely composed of stem lineages, despite the fact that phylogenetic evidence would suggest crown-group representatives should also be present in at least the Upper Cretaceous. It is impossible to base broad-reaching conclusions on the overall composition of the Cretaceous braconid fauna and possible changes in composition through time with such an underwhelming amount of material at hand. This reality stresses the need for fieldwork to discover new fossil deposits and material from existing localities, so we might build a grander picture of parasitoid evolution during the Mesozoic.

Acknowledgements

The authors thank two anonymous reviewers and Kees van Achterberg for their informative critiques which aided the improvement of the final paper. This project was supported by the International Scientific Partnership Program (ISPP) at King Saud University through ISPP #0083 (A.S.A. and M.S.E.), as well as by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB18030501), and the National Natural Science Foundation of China (91514302) (both to H.D.-Y.).

References

- Aguiar AP, Deans AR, Engel MS, Forshage M, Huber JT, Jennings JT, Johnson NF, Lelej AS, Longino JT, Lohrmann V, Mikó I, Ohl M, Rasmussen C, Taeger A, Yu DS (2013) Order Hymenoptera. Zootaxa 3073(1): 51–62. https://doi.org/10.11646/zootaxa.3703.1.12
- Azar D, Gèze R, Acra F (2010) Lebanese amber. In: Penney D (Ed.) Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, 271–298.
- Barden P, Grimaldi D (2013) A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). Zootaxa 3681(4): 405–412. https://doi.org/10.11646/ zootaxa.3681.4.5
- Barden P, Grimaldi D (2014) A diverse ant fauna from the mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). PLoS ONE 9(4): e93627 [1–20]. https://doi.org/10.1371/journal.pone.0093627
- Barden P, Grimaldi DA (2016) Adaptive radiation in socially advanced stem-group ants from the Cretaceous. Current Biology 26(4): 515–521. https://doi.org/10.1016/j.cub.2015.12.060
- Barden P, Herhold HW, Grimaldi DA (2017) A new genus of hell ants from the Cretaceous (Hymenoptera: Formicidae: Haidomyrmecini) with a novel head structure. Systematic Entomology 42(4): 837–846. https://doi.org/10.1111/syen.12253
- Basibuyuk HH, Rasnitsyn AP, van Achterberg K, Fitton MG, Quicke DLJ (1999) A new, putatively primitive Cretaceous fossil braconid subfamily from New Jersey amber (Hymenoptera, Braconidae). Zoologica Scripta 28(1–2): 211–214. https://doi.org/10.1046/j.1463-6409.1999.00006.x
- Belokobylskij SA (2009) A new enigmatic apterous cyclostome genus (Hymenoptera: Braconidae) from the Greek Islands. Annales de la Société Entomologique de France 45(1): 77–82. https://doi.org/10.1080/00379271.2009.10697591
- Belokobylskij SA (2012) Cretaceous braconid wasps from the Magadan Province of Russia. Acta Palaeontologica Polonica 57(2): 351–361. https://doi.org/10.4202/app.2010.0120
- Brues CT (1933) The parasitic Hymenoptera of the Baltic amber. Part I. Bernstein Forschungen 3: 4–178.
- Brues CT (1937) Superfamilies Ichneumonoidea, Serphoidea, and Chalcidoidea. University of Toronto Studies, Geological Series 40: 27–44.
- Brues CT (1939) New Oligocene Braconidae and Bethylidae from Baltic amber. Annals of the Entomological Society of America 32(2): 251–263. https://doi.org/10.1093/aesa/32.2.251

- Butcher BA, Zaldivar-Riverón A, van de Kamp T, dos Santos Rolo T, Baumbach T, Quicke DLJ (2014) Extension of historical range of Betylobraconinae (Hymenoptera: Braconidae) into Palaearctic Region based on a Baltic amber fossil, and description of a new species of *Mesocentrus* Szépligeti from Papua New Guinea. Zootaxa 3860(5): 449–463. https://doi.org/10.11646/zootaxa.3860.5.4
- Cruickshank RD, Ko K (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21(5): 441–455. https://doi.org/10.1016/ S1367-9120(02)00044-5
- Engel MS (1995) A new fossil snake-fly species from Baltic amber (Raphidioptera: Inocelliidae). Psyche 102(3–4): 187–193. https://doi.org/10.1155/1995/23626
- Engel MS (2014) An orchid bee of the genus *Eulaema* in Early Miocene Mexican amber (Hymenoptera: Apidae). Novitates Paleoentomologicae 7: 1–15. https://doi.org/10.17161/ np.v0i7.4726
- Engel MS (2016) Notes on Cretaceous amber Braconidae (Hymenoptera), with descriptions of two new genera. Novitates Paleoentomologicae 15: 1–7. https://doi.org/10.17161/ np.v0i15.5704
- Engel MS, Bennett DJ (2008) Anoblepsis, a new, bizarre braconid wasp genus in Dominican amber (Hymenoptera: Braconidae). Journal of the Kansas Entomological Society 81(4): 368–372. https://doi.org/10.2317/802.02.1
- Engel MS, Grimaldi DA (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). American Museum Novitates 3485: 1–23. https://doi.org/10.1206/0003-0082(2005)485[0001:PNAICA]2.0.CO;2
- Engel MS, Grimaldi DA (2007) The neuropterid fauna of Dominican and Mexican amber (Neuropterida: Megaloptera, Neuroptera). American Museum Novitates 3587: 1–58. https://doi.org/10.1206/0003-0082(2007)3587[1:TNFODA]2.0.CO;2
- Engel MS, Grimaldi DA (2008) Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). Nova Supplementa Entomologica 20: 1–86.
- Engel MS, Grimaldi DA (2009) Diversity and phylogeny of the Mesozoic wasp family Stigmaphronidae (Hymenoptera: Ceraphronoidea). Denisia 26: 53–68.
- Engel MS, Wang B (2016) The first Oriental protorhyssaline wasp (Hymenoptera: Braconidae): A new genus and species in Upper Cretaceous amber from Myanmar. Cretaceous Research 63: 28–32. https://doi.org/10.1016/j.cretres.2016.02.012
- Engel MS, Ortega-Blanco J, Soriano C, Grimaldi DA, Delclòs X (2013) A new lineage of engimatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). American Museum Novitates 3771: 1–23. https://doi.org/10.1206/3771.2
- Engel MS, Thomas JC, Alqarni AS (2017) A new genus of protorhyssaline wasps in Raritan amber (Hymenoptera, Braconidae). ZooKeys 711: 103–111. https://doi.org/10.3897/ zookeys.711.20709
- Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, Cambridge, UK, 755 pp.
- Grimaldi DA, Engel MS (2007) Why descriptive science still matters. BioScience 57(8): 646–647. https://doi.org/10.1641/B570802

- Grimaldi DA, Ross AJ (2017) Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser NC, Sues H-D (Eds) Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land. Dunedin Academic Press, Edinburgh, 287–342.
- Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361: 1–72. https://doi.org/10.1206/0003-0082(2002)361<0001:FC AFMB>2.0.CO;2
- Huber JT, Sharkey MJ (1993) Structure. In: Goulet H, Huber JT (Eds) Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada, Ottawa, 13–59.
- Kopylov DS (2011) Ichneumon wasps of the Khasurty locality in Transbaikalia (Insecta, Hymenoptera, Ichneumonidae). Paleontological Journal 45(4): 406–413. https://doi. org/10.1134/S0031030111040058
- Kopylov DS (2012) New species of Praeichneumonidae (Hymenoptera, Ichneumonoidea) from the Lower Cretaceous of Transbaikalia. Paleontological Journal 46(1): 66–72. https:// doi.org/10.1134/S0031030112010078
- Liu Z, Engel MS, Grimaldi DA (2007) Phylogeny and geological history of the cynipoid wasps (Hymenoptera: Cynipoidea). American Museum Novitates 3583: 1–48. https://doi. org/10.1206/0003-0082(2007)3583[1:PAGHOT]2.0.CO;2
- McKellar RC, Engel MS (2012) Hymenoptera in Canadian Cretaceous amber (Insecta). Cretaceous Research 35: 258–279. https://doi.org/10.1016/j.cretres.2011.12.009
- McKellar RC, Kopylov DS, Engel MS (2013a) Ichneumonidae (Insecta: Hymenoptera) in Canadian Late Cretaceous amber. Fossil Record 16(2): 217–227. https://doi.org/10.1002/ mmng.201300011
- McKellar RC, Glasier JRN, Engel MS (2013b) New ants (Hymenoptera: Formicidae: Dolichoderinae) from Canadian Late Cretaceous amber. Bulletin of Geosciences 88(3): 583–594. https://doi.org/10.3140/bull.geosci.1425
- McKellar RC, Glasier JRN, Engel MS (2013c) A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. Canadian Entomologist 145(4): 454–465. https://doi.org/10.4039/tce.2013.23
- Ortega-Blanco J, Bennett DJ, Delclòs X, Engel MS (2009) A primitive aphidiine wasp in Albian amber from Spain and a Northern Hemisphere origin for the subfamily (Hymenoptera: Braconidae: Aphidiinae). Journal of the Kansas Entomological Society 82(4): 273–282. https://doi.org/10.2317/JKES0812.08.1
- Ortega-Blanco J, Delclòs X, Engel MS (2011) A protorhyssaline wasp in Early Cretaceous amber from Spain (Hymenoptera: Braconidae). Journal of the Kansas Entomological Society 84(1): 51–57. https://doi.org/10.2317/JKES100728.1
- Perrichot V, Néraudeau D (2014) Introduction to thematic volume "fossil arthropods in Late Cretaceous Vendean amber (northwestern France)". Paleontological Contributions 10(A): 1–4.
- Perrichot V, Nel A, Quicke DLJ (2009) New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): Synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea. Zoologica Scripta 38(1): 79–88. https://doi. org/10.1111/j.1463-6409.2008.00358.x

- Perrichot V, Wang B, Engel MS (2016) Extreme morphogenesis and ecological specialization among Cretaceous basal ants. Current Biology 26(11): 1468–1472. https://doi. org/10.1016/j.cub.2016.03.075
- Quicke DLJ (2015) The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology. Wiley Blackwell, Oxford, 681 pp.
- Sharanowski BJ, Dowling APG, Sharkey MJ (2011) Molecular phylogenetics of Braconidae (Hymenoptera: Ichneumonoidea), based on multiple nuclear genes, and implications for classification. Systematic Entomology 36(3): 549–572. https://doi.org/10.1111/j.1365-3113.2011.00580.x
- Sharkey MJ, Wharton RA (1997) Morphology and terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World Genera of the Family Braconidae (Hymenoptera). International Society of Hymenopterists, Washington, DC, 19–37.
- Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M, Lei W, Li Q, Li X (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014
- Tobias VJ (1987) New taxa of braconids (Hymenoptera, Braconidae) from Baltic amber. Entomologicheskoe Obozrenie 66(4): 845–859. [In Russian]
- Townes H (1973) Two ichneumonids (Hymenoptera) from the Early Cretaceous. Proceedings of the Entomological Society of Washington 75(2): 216–219.
- van Achterberg C (1982) The fossil species of the subfamily Blacinae described by C.T. Brues (Hym.: Braconidae). Entomologische Berichten 42(6): 91–96.
- van Achterberg C (1984) Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea). Entomologisk Tidskrift 105(1–2): 41–58.
- van Achterberg C (1992) Revision of the genus *Histeromerus* Wesmael (Hymenoptera: Braconidae). Zoologische Mededelingen 66(9): 189–196.
- van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283: 1–189.
- van Achterberg C (2001) The first known fossil Masoninae (Hymenoptera: Braconidae) from Miocene Dominican amber. Zoologische Mededelingen 75(21): 393–396.
- Yu DSK, van Achterberg C, Horstmann K (2016) Taxapad 2016: Ichneumonoidea 2015 (biological and taxonomic information): Interactive Catalogue Database. Nepean, Ottawa. http://www.taxapad.com.
- Zhang H-C, Rasnitsyn AP (2003) Some ichneumonids (Insecta, Hymenoptera, Ichneumonoidea) from the Upper Mesozoic of China and Mongolia. Cretaceous Research 24(2): 193–202. https://doi.org/10.1016/S0195-6671(03)00031-4
- Zuparko RL, Poinar GO Jr (1997) *Aivalykus dominicanus* (Hymenoptera: Braconidae), a new species from Dominican amber. Proceedings of the Entomological Society of Washington 99(4): 744–747.

RESEARCH ARTICLE



Revision of the world species of the genus Habroteleia Kieffer (Hymenoptera, Platygastridae, Scelioninae)

Hua-yan Chen¹, Elijah J. Talamas², Lubomír Masner³, Norman F. Johnson^{1,4}

Department of Entomology, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212, U.S.A.
Florida Department of Agriculture and Consumer Services, The Doyle Conner Building, 1911 SW 34th St, Gainesville, Florida 32608, U.S.A. 3 Agriculture and Agri-Food Canada, K.W. Neatby Building, Ottawa, Ontario K1A 0C6, Canada 4 Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212, U.S.A.

Corresponding author: Norman F. Johnson (johnson.2@osu.edu)

Academic editor: J. Fernandez-Triana Received 24 October 2017 Accepted 27 December 2017	Published 17 January 2018

Citation: Chen H-y, Talamas EJ, Masner L, Johnson NF (2018) Revision of the world species of the genus *Habroteleia* Kieffer (Hymenoptera, Platygastridae, Scelioninae). ZooKeys 730: 87–122. https://doi.org/10.3897/zookeys.730.21846

Abstract

The genus Habroteleia Kieffer is revised. Seven species are recognized, three are redescribed: H. flavipes Kieffer, H. persimilis (Kozlov & Kononova), H. ruficoxa (Kieffer); and four species are described as new: H. mutabilis Chen & Talamas, **sp. n.**, H. salebra Chen & Talamas, **sp. n.**, H. soa Chen & Talamas, **sp. n.**, and H. spinosa Chen & Johnson, **sp. n.** Four species are treated as junior synonyms of Habroteleia flavipes Kieffer: Chrestoteleia bakeri Kieffer, **syn. n.**, Habroteleia bharatensis Saraswat, **syn. n.**, Habroteleia kotturensis (Sharma), **syn. n.** Habroteleia dagavia (Kozlov & Lê), **syn. n.** is treated as junior synonym of Habroteleia persimilis (Kozlov & Kononova). Baryconus vindhiensis (Sharma), **comb. n.** is transferred out of Habroteleia Kieffer. Habroteleia impressa (Kieffer) and H. scapularis (Kieffer) remain valid species but their identity and status are unclear.

Keywords

Platygastroidea, identification key, species description

Introduction

The genus *Habroteleia* was originally described by Kieffer (1905) based on the type species, *Habroteleia flavipes* Kieffer, collected on the island of Sumatra, Indonesia. Kieffer (1913) later proposed *Chrestoteleia* for a single species, *Chrestoteleia bakeri* Kieffer, collected from the Philippines, which was treated by Baltazar (1961) as a junior synonym of *Habroteleia*. Nine species have since been described from India, Japan and the Philippines. We here provide the first comprehensive treatment of the genus, including examination of type specimens of all species except *H. impressa* (Kieffer) and *H. scapularis* (Kieffer), for which we were unable to locate type material. The previously described species of *Habroteleia* were recorded from the Oriental region, extending from India to Japan, and we here provide records that expand the distribution of *Habroteleia* to include Madagascar, Papua New Guinea, and the Fijian archipelago.

The host of *Habroteleia* is unknown, but we suspect that it parasitizes orthopteran eggs (large and elongate) based on its elongate body and because Orthoptera is suspected to be the plesiomorphic host group for the platygastroids as a whole (Austin et al. 2005).

The contributions of the authors are as follows. H.-Y. Chen, E. J. Talamas and N.F. Johnson: character definition, generic concept development, species concept development, imaging, key development, manuscript preparation; L. Masner: character definition, generic concept development, species concept development. The authors of the new species are indicated in the heading of each description.

Materials and methods

This work is based upon specimens in the following collections, with abbreviations used in the text: BPBM, Bernice P. Bishop Museum, Honolulu, HI; CNCI, Canadian National Collection of Insects, Ottawa, Canada; CAS, California Academy of Sciences, San Francisco, CA; FSCA, Florida State Collection of Arthropods, Gainesville, FL; IEBR, Institute of Ecology and Biological Resourves, Hanoi, Vietnam; MCSN, Museo Civico de Storia Naturale "Giacomo Doria", Genoa, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; OSUC, C.A. Triplehorn Insect Collection, Ohio State University, Columbus, OH; SCAU, South China Agricultural University, Guangzhou, China; UCDC, R.M. Bohart Museum of Entomology, University of California, Davis, CA; ZIN, Zoological Museum, Academy of Sciences, St. Petersburg, Russia.

Abbreviations and morphological terms used in text: A1, A2, ... A12: antennomere 1, 2, ... 12; claval formula: distribution of the large, multiporous basiconic sensilla on the underside of apical antennomeres of the female, with the segment interval specified followed by the number of sensilla per segment (Bin, 1981); EH: eye height, length of compound eye measured parallel to dorsoventral midline of head; IOS: interocular space, minimal distance on frons between compound eyes; OD: ocellar diameter, greatest width of ocellus; OOL: ocular ocellar line, shortest distance from inner orbit

and outer margin of posterior ocellus (Masner 1980); T1, T2, ... T7: metasomal tergite 1, 2, ... 7; S1, S2, ... S7: metasomal sternite 1, 2, ... 7. Morphological terminology otherwise generally follows Masner (1980) and Mikó et al. (2007).

Morphological terms used in this work were as in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) (Appendix 1). Identifiers (URIs) in the format HAO_ XXXXXX represent concepts in the HAO and are provided to enable readers to confirm their understanding of the concepts being referenced. To learn more about a given concept, including additional images, notes, references and other metadata, use the identifier as a search term at http://glossary.hymao.org or use the identifier as a web-link.

In the Material Examined section the metadata for the specimens studied are recorded in an abbreviated format, using unique identifiers (numbers prefixed with "OSUC", "CASENT", "FBA", "MNHN_EY") for the individual specimens. The label data for all specimens have been georeferenced and recorded in the Hymenoptera Online database, and details on the data associated with these specimens can be accessed at the following link, hol.osu.edu, and entering the identifier in the form (note the space between the acronym and the number). The electronic version of the paper contains hyperlinks to external resources. Insofar as possible, the external information conforms to standards developed and maintained through the organization Biodiversity Information Standards (Taxonomic Database Working Group). All new species have been prospectively registered with Zoobank (Polaszek et al. 2005, www.zoobank.org), and other taxonomic names, where appropriate, have been retrospectively registered. The external hyperlinks are explicitly cited in the endnotes so that users of the printed version of this article have access to the same resources.

Data associated with the genus *Habroteleia* can be accessed at http://hol.osu.edu/ index.html?id=488. The generic and species descriptions were generated by a database application, vSysLab (vsyslab.osu.edu), designed to facilitate the production of a taxon by character data matrices, and to integrate those data with the existing taxonomic, media, and specimen-level database. Data may be exported in both text format and as input files for other applications. The text output for descriptions is in the format of "Character: Character state (s)". Polymorphic characters are indicated by semicolonseparated character states.

Images and measurements were produced with multiple systems. Photographs of IEBR specimens were captured with a Canon Rebel 600 camera connected to a Wild M10 microscope with a Fotoprojektiv 2.5×/SLR 10446175 adapter and stacked with the program Zerene Stacker. A scale bar was calibrated for images taken at the maximum magnification of the microscope. The remaining images were produced with Combine ZP and AutoMontage extended-focus software, using a JVC KY-F75U digital camera, Leica Z16 APOA microscope, and 1X objective lens. Images were postprocessed with Abobe Photoshop CS3 Extended. A standard set of images is provided for each species: dorsal habitus, lateral habitus, dorsal and lateral views of the head and mesosoma, and anterior view of head. The individual images are archived in Specimage (specimage.osu.edu), the image database at The Ohio State University.

Images of primary types of *H. ruficoxa* and *H. persimilis* were provided by Agnièle Touret-Alby (MNHN) and Konstantin Samartsev (ZIN), respectively. Images of the primary type of *Baryconus vindhiensis*, *Habroteleia bharatensis* and *Habroteleia kotturensis* were made available by Talamas et al. (2017) and images of *Triteleia dagavia* were made available by Talamas and Pham (2017), all are used in this publication with permission.

Taxonomy

Habroteleia Kieffer

Habroteleia Kieffer, 1905: 14 (original description. Type: Habroteleia flavipes Kieffer, by monotypy); Kieffer 1908: 114 (keyed); Brues 1908: 27, 38 (diagnosis, list of species, keyed); Kieffer 1910: 63, 69 (description, list of species, keyed); Kieffer 1913: 220 (description); Kieffer 1926: 267, 363 (description, keyed, key to species); Muesebeck and Walkley 1956: 357 (citation of type species); Baltazar 1961: 395 (synonymy); Baltazar 1966: 177 (cataloged, catalog of species of the Philippines); Masner 1976: 10, 26 (description, keyed); Mani and Sharma 1982: 155, 167 (description, keyed); Johnson 1992: 398 (cataloged, catalog of world species); Austin and Field 1997: 24, 68 (structure of ovipositor system, discussion of phylogenetic relationships, genus misplaced in Calliscelionini); Lê 2000: 31 (keyed); Kononova and Kozlov 2008: 23, 255 (description, keyed); Chen et al. 2013: 11 (keyed).

http://zoobank.org/CBFA7C74-68DD-44F2-BE05-AEBD88E6FA8D http://bioguid.osu.edu/xbiod_concepts/488

- Chrestoteleia Kieffer, 1913: 388 (original description. Type: Chrestoteleia bakeri Kieffer, by monotypy and original designation. Synonymized by Baltazar (1961)); Kieffer 1926: 271, 442 (description, keyed, key to species); Muesebeck and Walkley 1956: 342 (citation of type species); Baltazar 1961: 395 (junior synonym of Habroteleia Kieffer); Baltazar 1966: 182 (cataloged, catalog of species of the Philippines). http://zoobank.org/4EA90A05-D50A-42BF-B1C0-852F4B56FCBA http://bioguid.osu.edu/xbiod_concepts/8933
- *Crestoteleia* Kieffer: Kieffer 1916: 180 (key to new species described from the Philippines, spelling error).

Description. Length 2.18–5.18 mm; body moderately to markedly elongate, robust.

Head. Head shape in dorsal view: transverse. Hyperoccipital carina: absent. Occipital carina: present, complete or broadly interrupted medially. Anterior margin of occipital carina: crenulate. OOL: lateral ocellus nearly contiguous with inner orbits, OOL < 0.5 OD; lateral ocellus contiguous with inner orbit. Upper frons: convex, without frontal shelf or carina. Antennal scrobe: broadly convex or conave medially with distinct depression. Sculpture of antennal scrobe: smooth to punctate. Submedian carina:

absent. Orbital carina: absent. Inner orbits: diverging ventrally. IOS/EH: IOS distinctly less than EH. Interantennal process: short, often excavate medially. Central keel: present or absent. Antennal foramen: oriented laterally on interantennal process. Facial striae: absent. Malar sulcus: present. Setation of compound eye: absent. Gena: broad, convex, distinctly produced behind eye. Clypeus shape: narrow, slightly convex medially, lateral corners not produced. Anterior (or ventral) margin of clypeus: straight. Anteclypeus: absent. Postclypeus: absent. Labrum: not visible in anterior view. Number of mandibular teeth: 2. Arrangement of mandibular teeth: transverse. Number of maxillary palpomeres: 4. Shape of maxillary palpomeres: cylindrical. Number of labial palpomeres: 2.

Antenna. Number of antennomeres in female: 12. Number of antennomeres in male: 12. Insertion of radicle into A1: parallel to longitudinal axis of A1. Shape of A1: more or less cylindrical, not flattened. Length of A3 of female: distinctly longer than A2. Number of clavomeres in female antenna: 6. Number of antennomeres with multiporous plate sensilla in female: 5. Arrangement of doubled multiporous plate sensilla on female clava: in longitudinal pairs. Number of antennomeres bearing tyloids in male antenna: 0. Shape of male flagellum: filiform.

Mesosoma. Transverse pronotal carina: present anterior to epomial carina, present or absent posterior to epomial carina. Posterior apex of pronotum in dorsal view: straight, bifid apically to articulate with tegula. Epomial carina: present. Anterior face of pronotum: oblique, visible dorsally, short. Lateral face of pronotum: weakly concave below position of dorsal epomial carina. Netrion: present. Netrion shape: moderately wide, open ventrally. Anterior portion of mesoscutum: vertical, flexed ventrally to meet pronotum. Mesoscutum shape: pentagonal, excavate at base of wings. Skaphion: absent. Notauli: present, percurrent. Parapsidal lines: absent. Antero-admedian lines: absent. Transscutal articulation: well-developed, narrow. Shape of mesoscutellum: trapezoidal. Lateral mesoscutellar spine: absent. Median mesoscutellar spine: absent. Axillular spine: absent. Surface of mesoscutellum: convex throughout. Median longitudinal furrow on mesoscutellum: absent; present. Metascutellum: clearly differentiated. Form of metascutellum: transverse. Posterior margin of metascutellum: straight with a small projection medially. Setation of metascutellum: absent. Metapostnotum: not defined externally. Lateral propodeal projection: present. Median propodeal projection: present. Mesopleural carina: present. Mesal course of acetabular carina: not separating fore coxae. Mesopleural pit: present. Posterodorsal corner of mesopleuron: rounded anteriorly.

Legs. Number of mesotibial spurs: 1. Number of metatibial spurs: 1. Dorsal surface of metacoxa: smooth; punctate. Shape of metacoxa: cylindrical, ecarinate. Trochantellus: indicated by transverse sulcus on femur.

Wings. Wing development of female: macropterous. Wing development of male: macropterous. Tubular veins in fore wing: present. Bulla of fore wing R: absent. Length of marginal vein of fore wing: more than twice as long as stigmal vein. Origin of r-rs in fore wing: arising from marginal vein along costal margin. Basal vein (Rs+M) in fore wing: absent. Development of R vein in hind wing: complete.

Metasoma. Number of external metasomal tergites in female: 6. Number of external metasoma sternites in female: 6. Number of external metasomal tergites in male:

8. Number of external metasomal sternites in male: 8. Shape of metasoma: lanceolate. Laterotergites: present, narrow. Laterosternites: present. T1 of female: flat; medially convex as a small hump anteriorly. Relative size of metasomal segments: T3 longest, T2 and T4 subequal in length. Metasomal tergites with basal crenulae: T2. Sublateral carinae on tergites: absent. Median longitudinal carina on metasomal terga: absent. Shape of female T6: flattened. Anterior margin of S1: not produced anteriorly, straight. Felt fields: absent. Ovipositor: *Ceratobaeus*-type (Austin and Field 1997).

Diagnosis. *Habroteleia* can be separated from other scelionines by the combination of the following characters: epomial carina present; malar and facial striae absent; marginal vein many times longer than stigmal vein; postmarginal vein (R1) absent or rudimentary; propodeum with lateral and median projections; T6 in females strongly depressed dorsoventrally to form a flat triangle; male antenna without tyloid (Chen et al. 2013).

The wing venation and large size of Habroteleia make it a relatively easy genus to identify. In all species of Habroteleia the marginal vein is many times longer than the stigmal vein and the postmarginal vein is very short or absent. Macroteleia and Triteleia share the presence of a long marginal vein, though in the latter genus it is variable and the marginal and stigmal veins can be of similar length. However, both Macroteleia and Triteleia have a well-developed postmarginal vein. Habroteleia also differs from these genera in that it has a *Ceratobaeus*-type ovipositor (Austin and Field 1997). The complexity of this system suggests that while these three genera are quite similar in external appearance, in fact they may not be closely related at all. Alternatively, it implies that the ovipositor system is much more labile than expected. Unfortunately, Habroteleia was not included among the taxa in the phylogenetic analysis of Murphy et al. (2007), and we therefore do not have an independent assessment of its relations. The structure of the ovipositor is of limited use for separating Habroteleia from Triteleia because it is rarely extruded in preserved specimens of the latter, and it is not obvious from external morphology (e.g. visibility of T7 in females) that *Habroteleia* has a *Ceratobaeus*-type ovipositor. Chen et al. (2013) provided a key to separate these genera which we here present again.

Key to separate Macroteleia, Triteleia and Habroteleia

1	Postmarginal vein in fore wing absent or rudimentary; ovipositor Ceratobae-
	us-type
_	Postmarginal vein in fore wing well developed, distinctly longer than stigma
	vein (r-rs); ovipositor <i>Scelio</i> -type2
2	Female T6 strongly compressed laterally, wedge-like; male apical tergite api-
	cally emarginate or with 1 central spine but never bispinose
_	Female T6 triangular, not compressed laterally; male apical tergite with pos-
	terolateral conrners bispinose or at least pointed Triteleia Kieffer

Key to females

(unknown for *H. ruficoxa* (Kieffer))

1	T1 with horn (Figs 14, 20, 26, 32, 38, 62, 76)2
_	T1 without horn (Figs 16, 22, 79, 87)
2	Posterior vertex largely smooth with sparse to moderate punctures above oc-
	cipital carina (Fig. 74); gena sparsely punctate (Fig. 72); mesepisternum an-
	teroventral to mesopleural depression largely smooth with sparse punctures
	(Fig. 72) Habroteleia salebra Chen & Talamas, sp. n.
_	Posterior vertex densely punctate to punctate rugose (Figs 13, 20, 26, 32, 38,
	61); gena densely punctate to punctate rugose (Figs 12, 18, 24, 30, 36, 60);
	mesepisternum anteroventral to mesopleural depression densely punctate to
	punctate rugose (Figs 12, 18, 24, 30, 36, 60) 3
3	Median propodeal projection short (Figs 14, 20, 26, 32, 38); T6 in female
	longitudinally striate, with fine punctures in interstices (Fig. 88)
-	Median propodeal projection long (Figs 56, 62); T6 in female densely punc-
	tate and without longitudinal striae (Fig. 89)
4	Central keel of frons present (Figs 80, 86); upper frons densely punctate (Figs
	80, 86); transverse sulcus on T2 present (Figs 79, 87)5
-	Central keel of frons absent (Figs 45, 51); upper frons sparsely punctate (Figs
	45, 51); transverse sulcus on T2 absent (Figs 16, 22)
5	Apex of T6 in female rounded (Fig. 81); posterior vertex punctate rugose
	(Fig. 80) Habroteleia soa Chen & Talamas, sp. n.
-	Apex of T6 in female with small spine (Fig. 5); posterior vertex smooth with
	sparse punctures (Fig. 85) Habroteleia spinosa Chen & Johnson, sp. n.

Key to males

1	Apex of T8 with apical spine (Fig. 3)2
_	Apex of T8 without apical spine (Fig. 4)
2	Occipital carina interrupted medially (Fig. 74); posterior vertex largely smooth
	with sparse to moderate punctures above occipital carina (Fig. 74); gena sparsely
	punctate (Fig. 72)
_	Occipital carina complete (Figs 14, 20, 26, 32, 38, 80); posterior vertex
	densely punctate or punctate rugose (Figs 14, 20, 26, 32, 38, 79); gena dense-
	$(E^{*}_{1})^{2}$

3 Central keel absent (Figs 21, 27); netrion rugulose anteriorly, smooth posteriorly, sometimes smooth only along posterior margin (Fig. 6); T1 densely longitudinally striate with rugulose interstices (Figs 22, 34, 40) Central keel present (Fig. 80); netrion coarsely striate (Fig. 78); T1 sparsely longitudinally striate, smooth in interstices (Fig. 79)..... Central keel absent (Figs 45, 51); transverse sulcus on T2 absent (Figs 46, 4 Central keel present (Figs 57, 69, 86); transverse sulcus on T2 present (Figs **64**, 70, 87).....**5** Median propodeal projection long (Figs 56, 60, 62); notaulus formed by 5 contiguous punctures (Figs 56, 61) Median propodeal projection short (Figs 66, 85); notaulus formed by discrete punctures (Figs 68, 85)7 Posterior vertex punctate rugose (Fig. 68); mesoscutal midlobe densely punc-7 tate (Fig. 68); gena punctate rugose throughout (Fig. 66) Posterior vertex smooth with sparse punctures (Fig. 85); mesoscutal midlobe densely and finely punctate along anterior margin, otherwise smooth (Fig. 85): gena sparsely punctate (Fig. 83)

Baryconus vindhiensis (Sharma), comb. n.

http://zoobank.org/0EC31368-F49B-4183-B2C5-BD09C1C07753 http://bioguid.osu.edu/xbiod_concepts/4540 Figures 7–10

Triteleia vindhiensis Sharma, 1981: 451 (original description); Mani and Sharma 1982: 168 (description, generic transfer).

Habroteleia vindhiensis (Sharma): Johnson 1992: 399 (cataloged, type information).

Link to distribution map. [http://hol.osu.edu/map-large.html?id=4540]

Material examined. Holotype, female, *T. vindhiensis*: **INDIA**: Madhya Pradesh St., 21.5, Panna-Satna Road, 9.IX–10.IX.1979, M. S. Mani et al., USNMENT01197073 (deposited in USNM).

Comments. The deep frontal depression margined by a sharp carina (Fig. 8), pronounced occiput (Fig. 9), long postmarginal vein and short marginal vein (Fig. 9) clearly indicate that this species belongs to *Baryconus*.

Habroteleia flavipes Kieffer

http://zoobank.org/ACD49F55-9F4E-4C91-A044-22DCC0428FF6 http://bioguid.osu.edu/xbiod_concepts/4535 Figures 6, 11–40, 88

- *Habroteleia flavipes* Kieffer, 1905: 15 (original description, keyed); Kieffer 1926: 363 (description, keyed); Bin 1974: 455 (type information); Johnson 1992: 399 (cataloged, type information).
- Habroteleia browni Crawford, 1910: 125 (original description); Kieffer 1926: 363, 364 (description, keyed); Baltazar 1966: 177 (cataloged, synonymy, type information, distribution); Masner and Muesebeck 1968: 37 (type information); Johnson 1992: 399 (cataloged, type information), syn. n.

http://zoobank.org/EC09DB18-92D9-4FB1-B986-3F7EAD7D54E4 http://bioguid.osu.edu/xbiod_concepts/4534

- *Chrestoteleia Bakeri* Kieffer, 1913: 389 (original description); Kelner-Pillault 1958: 150 (type information); Johnson 1992: 399 (type information), **syn. n.** http://zoobank.org/F18A3905-9A5A-4755-A56A-5379E8564044 http://bioguid.osu.edu/xbiod_concepts/8935
- *Chrestoteleia bakeri* Kieffer: Kieffer, 1926: 443 (description, keyed); Baltazar 1966: 177 (junior synonym of *Habroteleia browni* Crawford); Baltazar 1966: 182 (cataloged, type information, distribution).
- Habroteleia bakeri (Kieffer): Baltazar 1961: 395 (generic transfer, diagnosis).
- Habroteleia bharatensis Saraswat, 1978: 7 (original description); Mani and Sharma 1982: 167 (description); Johnson 1992: 398 (cataloged), syn. n. http://zoobank.org/309A96B1-1DCA-45CA-B1AB-1D6E570C7E07 http://bioguid.osu.edu/xbiod_concepts/4533
- *Triteleia kotturensis* Sharma, 1981: 447 (original description), **syn. n.** http://zoobank.org/28DFECE9-8723-4ACA-BB61-96B11C9546A8 http://bioguid.osu.edu/xbiod concepts/8940
- *Habroteleia kotturensis* (Sharma): Mani and Sharma 1982: 168 (description, generic transfer); Johnson 1992: 399 (cataloged, type information)

Description. Body length of female: 4.36–4.72 mm (n=20). Body length of male: 4.15–4.52 mm (n=20). Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: dense. Sculpture of antennal scrobe: punctate rugose to smooth. Central keel: absent. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: complete. Sculpture of posterior vertex: densely punctate to punctate rugose. Sculpture of gena: densely punctate to punctate rugose.

Color of mesosoma: black. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: densely punctate. Sculpture of netrion: anterior half rugulose, posterior half smooth. Setae of netrion: dense throughout. Sculpture of notaulus: contiguously punctate. Sculpture of mesoscutal midlobe: largely punctate



Figures 1–6. 1–2 *Habroteleia mutabilis* sp. n. 1 Paratype (FBA 143219), Propodeum, dorsolateral view 2 Holotype (FBA 070892), Propodeum, dorsolateral view 3 *Habroteleia salebra* sp. n., male, paratype (OSUC 688063), Apex of metasoma, dorsal view 4 *Habroteleia spinosa* sp. n., male, paratype (OSUC 232878), Apex of metasoma, dorsal view 5 *Habroteleia spinosa* sp. n., female, holotype (OSUC 232889), Apex of metasoma, dorsal view 6 *Habroteleia flavipes*, male (OSUC 58007), Pronotum, lateral view.

rugose, with a medial furrow and smooth areas laterally. Sculpture of lateral lobe of mesoscutum: sparsely punctate. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: dense. Sculpture of mesoscutellum: coarsely punctate rugose. Median propodeal projection: short. Mesopleural carina: distinct. Sculpture of mesopleural depression: punctate rugose. Sculpture of dorsal metapleural area: smooth to rugulose. Sculpture of ventral metapleural area: punctate rugose.



Figures 7–10. *Baryconus vindhiensis*, female, holotype (USNMENT01197073). 7 Lateral habitus 8 Head, lateral view 9 Dorsal habitus 10 Labels.

gose. Setation of ventral metapleural area: dense. Color of legs: orange-yellow to dark brown; dark brown to black. Sculpture of hind coxa: densely punctate.

Color of metasoma: black; black with T3–T4 and S2–S5 partly brown to yellow. T1 horn in female: present. Sculpture of posterior margin of T1 in female: densely longitudinally striate, punctate rugulose in interstices. Transverse sulcus on T2: present. Sculpture of T2–T5: densely longitudinally striate, with fine punctures in interstices. Sculpture of T6 in female: densely longitudinally striate, with fine punctures in interstices. Length of T6 in female: distinctly longer than wide. Apex of T6 in female: round. Sculpture of S2: longitudinally striate rugose. Sculpture of T1 in male: densely longitudinally striate, punctate rugulose in interstices. Male T8 apical spine: present.

Diagnosis. This species is most similar to *H. persimilis* but can be distinguished by its short median propodeal projection and longitudinally striate T6 in female.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=4535]

Material examined. Holotype of *Habroteleia flavipes* Kieffer, female: INDONE-SIA: Sumatera Utara Prov., Sumatra Isl., Pangherang Pisang, X.1890 – III.1891, E. Modigliani, MCSN 0001 (deposited in MCSN). Holotype of *Habroteleia bharatensis* Saraswat, female: INDIA: West Bengal St., 16.4, Poro North, 6.IV–24.IV.1976, M. S. Mani, USNMENT01197132 (deposited in USNM). Syntype of *Chrestoteleia bakeri* Kieffer, female: PHILIPPINES: Laguna Prov., Los Baños, no date, Baker, ANIC



Figures 11–16. *Habroteleia flavipes*, female, holotype (MCSN 0001). 11 Lateral habitus 12 Head and mesosoma, lateral view 13 Dorsal habitus 14 Head and mesosoma, dorsal view 15 Head, lateral view 16 Metasoma and wings, dorsal view.

DB 32-020728 (deposited in ANIC). Syntype of *Chrestoteleia Bakeri* Kieffer, female: **PHILIPPINES**: Laguna Prov., Los Baños, no date, Baker, MNHN 0013 (deposited in MNHN). Holotype of *Habroteleia browni* Crawford, female: **PHILIPPINES**: Metropolitan Manila Reg., Manila, no date, R. Brown, USNM Type No. 12894 (deposited in USNM). Holotype of *Triteleia kotturensis* Sharma, female: **INDIA**: Kerala St., 24.8, Kottur, 4.X.1980, M. S. Mani et al., USNMENT01197074 (deposited in USNM). *Other material*: (137 females, 79 males, 1 unknown) **BANGLADESH**: 2 females, OSUC 688056–688057 (CNCI). **BRUNEI**: 1 female, OSUC 232932 (BPBM). **CAM**-



Figures 17–22. *Habroteleia bharatensis*, female, holotype (USNMENT01197132). 17 Lateral habitus 18 Head and mesosoma, lateral view 19 Dorsal habitus 20 Head and mesosoma, dorsal view 21 Head, anterior view 22 Metasoma, dorsal view.

BODIA: 1 female, OSUC 232935 (BPBM). **CHINA**: 23 females, 7 males, OSUC 232920 (BPBM); SCAU 2010100389, 2010100402, 2010100419, 2010100431, 2010100437, 2010100445–2010100446, 2010100459, 2010100464, 2010100495, 2010100497, 2010100504, 2010100504–2010100505, 2010100508–2010100512, 2010100514, 2010100517–2010100518, 2010100521–2010100522, 2010100524–2010100526, 2010100552 (SCAU). **INDIA**: 1 male, OSUC 688053 (CNCI). **INDONESIA**: 58 females, 23 males, OSUC 232906 (BPBM); OSUC 687960–688009, 688014–688041 (CNCI); OSUC 58007–58008 (OSUC). **LAOS**:



Figures 23–28. *Habroteleia browni*, female, holotype (USNM Type No. 12894). 23 Lateral habitus 24 Head and mesosoma, lateral view 25 Dorsal habitus 26 Head and mesosoma, dorsal view 27 Head, anterior view 28 Metasoma and wings, dorsal view.

2 females, 3 males, OSUC 687955–687959 (CNCI). **MALAYSIA**: 23 females, 26 males, OSUC 232907–232914, 232916–232919, 232923, 232931, 232933-232934, 232937, 246583 (BPBM); OSUC 687944–687954, 688058-688059 (CNCI); OSUC 491881–491896, 536427 (OSUC); OSUC 179084 (UCDC). **PHILIP-PINES**: 1 female, 3 males, OSUC 232925–232928 (BPBM). **SOUTH KOREA**: 7 females, 2 males, 1 unknown, OSUC 687939 (CNCI); USNMENT01335741, 01335743–01335745, 01335747–01335749 (FSCA); USNMENT01335740, 01335742 (OSUC). **SRI LANKA**: 1 male, OSUC 688055 (CNCI). **THAILAND**:



Figures 29–34. *Chrestoteleia bakeri*, female, holotype (MNHN 0013). 29 Lateral habitus 30 Head and mesosoma, lateral view 31 Dorsal habitus 32 Head and mesosoma, dorsal view 33 Head, anterior view 34 Metasoma and wings, dorsal view.

16 females, 13 males, OSUC 232921–232922, 232924 (BPBM); OSUC 688042, 688049–688051 (CNCI); OSUC 321998–322002, 370249, 374199–374201, 381766–381770, 688080–688087 (OSUC). **VIETNAM**: 3 females, OSUC 232915 (BPBM); OSUC 688052 (CNCI); OSUC 284756 (OSUC).

Comments. The metasomal color in *H. flavipes* varies from entirely dark brown to having T3–T4 and S2–S5 mostly yellow, apparently without any correlation with geography. In males, the length of the spine at the apex of T8 varies from short to long, but it is always present.



Figures 35–40. *Habroteleia kotturensis*, female, holotype (USNMENT01197074). 35 Lateral habitus 36 Head and mesosoma, lateral view 37 Dorsal habitus 38 Head and mesosoma, dorsal view 39 Head, lateral view 40 Metasoma and wings, dorsal view.

Habroteleia impressa (Kieffer)

http://zoobank.org/5A7AAB83-B2A4-401F-A137-D96D29D7648E http://bioguid.osu.edu/xbiod_concepts/4536

Crestoteleia impressa Kieffer, 1916: 180, 181 (original description, keyed, spelling error). *Chrestoteleia impressa* Kieffer: Kieffer 1926: 443 (description, keyed); Baltazar 1966: 182 (cataloged, distribution).

Habroteleia impressa (Kieffer): Baltazar 1966: 177 (cataloged, generic transfer, distribution); Johnson 1992: 399 (cataloged, type information).

Comments. We were unable to locate the type specimens of this species, and its status and identity are unclear.

Habroteleia mutabilis Chen & Talamas, sp. n. http://zoobank.org/5ADA1AD2-2B82-4314-A7A6-E65EBDBBE561 http://bioguid.osu.edu/xbiod_concepts/448460 Figures 1–2, 41–52

Description. Body length of female: 3.60–3.74 mm (n=20). Body length of male: 3.36–3.72 mm (n=20). Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: sparse. Sculpture of antennal scrobe: foveate. Central keel: absent. Sculpture of ventrolateral frons: denstly punctate. Occipital carina: complete. Sculpture of posterior vertex: punctate rugose. Sculpture of gena: punctate rugose ventrally, sparsely punctate dorsally. Sculpture of occiput: smooth.

Color of mesosoma: black; orange. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: smooth anteriorly, foveate posteriorly. Sculpture of netrion: coarsely striate. Setae of netrion: sparse throughout. Sculpture of notaulus: discretely punctate. Sculpture of mesoscutal midlobe: coarsely carinate with two rows of contiguous coarse punctures; largely smooth, with two rows of discrete coarse punctures. Sculpture of lateral lobe of mesoscutum: smooth. Sculpture of lateral propodeal area: foveate. Setation of mesoscutellum: sparse. Sculpture of mesoscutellum: sparsely punctate. Median propodeal projection: short; long. Mesopleural carina: distinct. Sculpture of mesopleural carina. Sculpture of dorsal metapleural area: smooth. Sculpture of ventral metapleural area: smooth to foveate. Setation of ventral metapleural area: sparse. Color of legs: orange-yellow to dark brown; dark brown to black. Sculpture of hind coxa: smooth.

Color of metasoma: black; orange with dark brown to black patches. T1 horn in female: absent. Sculpture of posterior margin of T1 in female: sparsely longitudinally striate. Transverse sulcus on T2: absent. Sculpture of T2–T5: T2–T3 sparsely longitudinally striate throughout, T4–T5 smooth medially, longitudinally striate. Sculpture of T6 in female: smooth. Length of T6 in female: wider than long. Apex of T6 in female: round. Sculpture of S2: sparsely longitudinally striate. Sculpture of T1 in male: sparsely longitudinally striate, smooth in interstices. Male T8 apical spine: absent.

Etymology. The epithet is inspired by the Latin word for changeable, in reference to the variations in body color, sculpture of mesoscutal midlobe, and the length of median propodeal projection, and is intended to be treated as an adjective.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=448460]



Figures 41–46. *Habroteleia mutabilis* sp. n., female, holotype (FBA 142603). 41 Lateral habitus 42 Head and mesosoma, lateral view 43 Dorsal habitus 44 Head and mesosoma, dorsal view 45 Head, anterior view 46 Metasoma and wings, dorsal view.

Material examined. Holotype, female: **FIJI**: Northern Div., Bua Prov., Vanua Levu Isl., 6km NW Kilaka Village, MT5, 98m, 16.807°S, 178.991°E, Batiqere Range, 28.VI–21.VII.2004, Malaise trap, Schlinger & Tokota'a, FBA 142603 (deposited in BPBM). *Paratypes*: **FIJI**: 53 females, 27 males, FBA 070892, OSUC 232898, OSUC 232901, OSUC 232902, OSUC 232903, OSUC 232904, OSUC 232905 (BPBM); FBA 014394, 014404, 014409, 014413-014414, 019832, 025807, 025815, 029311, 029313, 029315, 029318-029320, 029323, 032077, 032086, 036322, 036328, 047849, 047855, 058998, 059005, 059026, 070887, 070893-070894, 082922, 084174-084175,



Figures 47–52. *Habroteleia mutabilis* sp. n., female, paratype (FBA 070892). 47 Lateral habitus 48 Head and mesosoma, lateral view 49 Dorsal habitus 50 Head and mesosoma, dorsal view 51 Head, anterior view 52 Metasoma and wings, dorsal view.

084181, 084183, 088442, 094483, 094485, 094487, 099217, 101111, 101129, 101568, 140945, 140956, 140961, 142806, 143124, 143130, 143134, 143209, 143217-143219, 144459, 151785, 151788, 164303, 166124, 166126, 166129, 166160, 166162-166163, 179833, 179838, 182136, 182139-182140, 182142, 186114, 188585, 188680, OSUC 688078, OSUC 688161, OSUC 688162 (CNCI). *Other material:* **FIJI**: 1 female, 1 male, OSUC 232900 (BPBM); FBA 084185 (CNCI).

Comments. This species is well supported by many characters, although the color of mesosoma and metasoma, sculpture of mesoscutal midlobe, and the length of median

propodeal projection are variable. The color of mesosoma and metasoma varies from orange to dark brown. The sculpture of the mesoscutal midlobe varies from largely smooth with two rows of discrete coarse punctures to coarsely carinate with two rows of contiguous coarse punctures. The length of the median propodeal projection varies from short to long. These variations are gradual among specimens. Therefore, we consider them as intraspecific rather than interspecific differences.

Habroteleia persimilis (Kozlov & Kononova)

http://zoobank.org/F7A438F7-5207-4305-9467-11E23AA0923F http://bioguid.osu.edu/xbiod_concepts/243852 Figures 53–64, 89–90

- *Triteleia persimilis* Kozlov & Kononova, 1985: 15, 17 (original description. Keyed); Kozlov and Kononova 1990: 174, 178 (description, keyed); Johnson 1992: 509 (cataloged, type information); Kononova 1995: 69 (keyed); Kononova and Petrov 2000: 28 (keyed).
- *Habroteleia persimilis* (Kozlov & Kononova): Kononova and Kozlov 2008: 255 (description, generic transfer).
- *Triteleia dagavia* Kozlov & Lê, 1995: 441, 445 (original description, keyed); Kozlov and Lê 1996: 9, 14 (described as new, keyed); Lê 2000: 76, 341 (description, keyed, type information), **syn. n.**

http://zoobank.org/451262B6-B23F-487F-A870-AAB91CB1E35A

http://bioguid.osu.edu/xbiod_concepts/28154

Habroteleia dagavia (Kozlov & Lê): Talamas and Pham 2017: 227 (type information, generic transfer).

Description. Body length of female: 4.75-5.18 mm (n=20). Body length of male: 4.25-4.74 mm (n=20). Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: dense. Sculpture of antennal scrobe: punctate rugose to smooth. Central keel: present. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: complete. Sculpture of posterior vertex: punctate rugose. Sculpture of gena: punctate rugose. Sculpture of occipital carine.

Color of mesosoma: black. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: smooth anteriorly, foveate posteriorly. Sculpture of netrion: coarsely striate. Setae of netrion: sparse throughout. Sculpture of notaulus: contiguously punctate. Sculpture of mesoscutal midlobe: largely densely punctate, with a medial furrow and smooth areas laterally. Sculpture of lateral lobe of mesoscutum: sparsely punctate. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: dense. Sculpture of mesoscutellum: coarsely punctate rugose. Median propodeal projection: long. Mesopleural carina: distinct. Sculpture of mesopleural area: tral to mesopleural depression: punctate rugose. Sculpture of dorsal metapleural area:



Figures 53–58. *Triteleia persimilis*, female, holotype (ZMAS 0139). 53 Lateral habitus 54 Head and mesosoma, lateral view 55 Dorsal habitus 56 Mesosoma, dorsal view 57 Head, anterior view 58 Metasoma, dorsal view.

smooth. Sculpture of ventral metapleural area: rugose. Setation of ventral metapleural area: dense. Color of legs: orange-yellow. Sculpture of hind coxa: densely punctate.

Color of metasoma: black. T1 horn in female: present. Sculpture of posterior margin of T1 in female: largely longitudinally striate with horn punctate rugose. Transverse sulcus on T2: present. Sculpture of T2–T5: densely longitudinally striate, with fine punctures in interstices. Sculpture of T6 in female: densely punctate. Length of T6 in female: distinctly longer than wide. Apex of T6 in female: round. Sculpture of S2:



Figures 59–64. *Triteleia dagavia*, female, holotype (IEBR 0143). 59 Lateral habitus 60 Head and mesosoma, lateral view 61 Head and mesosoma, dorsal view 62 Propodeum, dorsolateral view 63 Head, lateral view 64 Metasoma, dorsal view.

densely longitudinally striate, punctate in interstices. Sculpture of T1 in male: densely longitudinally striate, punctate rugulose in interstices. Male T8 apical spine: absent.

Diagnosis. This species is most similar to *H. flavipes* but can be distinguished by its long median propodeal projection and densely punctate T6 in female.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=243852]

Material examined. Holotype, female, *T. persimilis*: JAPAN: Aichi Pref., Honshu Isl., Inuyama City, 6.X.1981, E. Sugonyaev, ZIN 0014 (deposited in ZIN). Holotype of *Triteleia dagavia* Kozlov & Lê, female: VIETNAM: Quang Nam Prov., Lang
Stream, forest, Dak Pring, 31.X.1979, X. H. Lê, IEBR 0143 (deposited in IEBR). *Other material*: (48 females, 43 males) **CHINA**: 6 females, 10 males, SCAU 2010100315–2010100317, 2010100319–2010100320, 2010100322, 2010100330, 2010100335, 2010100337–2010100340, 2010100347, 2010100349, 2010100352–2010100353 (SCAU). **JAPAN**: 40 females, 29 males, OSUC 687863, 687865–687909, 687914–687936 (CNCI). **SOUTH KOREA**: 2 females, 4 males, OSUC 687937–687938, 687940–687943 (CNCI).

Comments. *Habroteleia persimilis*, like *H. flavipes*, has a distribution that spans a large latitudinal range, extending from central Vietnam into the Palearctic region in Japan and South Korea.

Habroteleia ruficoxa (Kieffer)

http://zoobank.org/C3EF6C6D-486C-47FC-B481-81EDF21FA806 http://bioguid.osu.edu/xbiod_concepts/4538 Figures 65–70

- *Phaedroteleia ruficoxa* Kieffer, 1916: 182, 183 (original description. Keyed); Kieffer 1926: 418 (description, keyed); Kelner-Pillault 1958: 151 (type information); Baltazar 1966: 181 (cataloged, type information, distribution).
- Habroteleia ruficoxa (Kieffer): Masner 1976: 26 (generic transfer); Johnson 1992: 399 (cataloged, type information).

Description. Body length of male: 4.0 mm (n=1). Length of A3 in male: as long as A2. Punctation of frons above antennal scrobe: sparse. Sculpture of antennal scrobe: foveate. Central keel: present. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: complete. Sculpture of posterior vertex: punctate rugose. Sculpture of gena: punctate rugose. Sculpture of occiput: smooth.

Color of mesosoma: black. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: smooth anteriorly, foveate posteriorly. Sculpture of netrion: coarsely striate. Setae of netrion: dense throughout. Sculpture of notaulus: discretely punctate. Sculpture of mesoscutal midlobe: densely punctate. Sculpture of lateral lobe of mesoscutum: sparsely punctate. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: sparse. Sculpture of mesoscutellum: sparsely punctate. Median propodeal projection: short. Mesopleural carina: distinct. Sculpture of mesepisternum anteroventral to mesopleural depression: largely smooth with sparse punctures. Sculpture of dorsal metapleural area: rugose. Sculpture of ventral metapleural area: rugose. Setation of ventral metapleural area: color of legs: orangeyellow. Sculpture of hind coxa: densely punctate.

Color of metasoma: black. Transverse sulcus on T2: present. Sculpture of T2–T5: sparsely longitudinally striate, smooth in interstices. Sculpture of T1 in male: sparsely longitudinally striate, smooth in interstices. Male T8 apical spine: absent.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=4538]



Figures 65–70. *Phaedroteleia ruficoxa*, male, holotype (MNHN_EY3427). 65 Lateral habitus 66 Head and mesosoma, lateral view 67 Dorsal habitus 68 Head and mesosoma, dorsal view 69 Head, anterior view 70 Metasoma, dorsal view.

Material examined. Holotype, male, *P. ruficoxa*: PHILIPPINES: Mindanao Isl., Butuan Chartered City, no date, Baker, MNHN_EY3427 (deposited in MNHN).

Comments. The holotype specimen of *Habroteleia ruficoxa* is in reasonably good condition in that the characters used for diagnosis at the species level are readily accessible. The challenge is that the species was described from a single male and in the course of this revision we did not encounter any additional specimens of *H. ruficoxa*. The absence of a spine on T8 in the male, the largely smooth surface of the mesos-

cutum and mesoscutellum, and the notauli weakly indicated by punctures place the holotype specimen well outside of our concept of *H. flavipes*, the only other species of *Habroteleia* known from the Philippines.

Habroteleia salebra Chen & Talamas, sp. n. http://zoobank.org/F60BFB76-6AA1-4484-B2C7-CA6BE93CED9F http://bioguid.osu.edu/xbiod_concepts/448456 Figures 3, 71–76

Description. Body length of female: 4.28–4.90 mm (n=20). Body length of male: 4.30–4.73mm (n=20). Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: sparse. Sculpture of antennal scrobe: smooth. Central keel: absent. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: interrupted medially. Sculpture of posterior vertex: smooth with sparse punctures. Sculpture of gena: sparsely punctate. Sculpture of occiput: densely finely punctate.

Color of mesosoma: black. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: smooth anteriorly, foveate posteriorly. Sculpture of netrion: coarsely striate. Setae of netrion: sparse throughout. Sculpture of notaulus: discretely punctate. Sculpture of mesoscutal midlobe: densely and finely punctate along anterior margin, sparsely punctate along posterior margin, otherwise smooth. Sculpture of lateral lobe of mesoscutum: smooth. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: sparse. Sculpture of mesoscutellum: coarsely punctate rugose. Median propodeal projection: short. Mesopleural carina: weakly developed. Sculpture of mesepisternum anteroventral to mesopleural depression: largely smooth with sparse punctures. Sculpture of dorsal metapleural area: smooth. Sculpture of ventral metapleural area: punctate rugose. Setation of ventral metapleural area: dense. Color of legs: dark brown to black. Sculpture of hind coxa: densely punctate.

Color of metasoma: black. T1 horn in female: present. Sculpture of posterior margin of T1 in female: densely longitudinally striate, punctate rugulose in interstices. Transverse sulcus on T2: present. Sculpture of T2–T5: densely longitudinally striate, with fine punctures in interstices. Sculpture of T6 in female: densely punctate. Length of T6 in female: distinctly longer than wide. Apex of T6 in female: round. Sculpture of S2: sparsely longitudinally striate medially, with fine punctures in interstices, irregularly finely punctate laterally. Sculpture of T1 in male: densely longitudinally striate, punctate rugulose in interstices. Male T8 apical spine: present.

Diagnosis. This species is most similar to *H. spinosa* but can be distinguished by the round apex of T6 in females and the absence of a spine on the apex of T8 in males.

Etymology. The epithet is inspired by the Latin word for a rough, uneven road, in reference to the glabrous netrion sulcus adjacent to the setose posterior portion of the netrion, and is intended to be treated as a noun in apposition.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=448456]



Figures 71–76. *Habroteleia salebra* sp. n., female, holotype (OSUC 688076). 71 Lateral habitus 72 Head and mesosoma, lateral view 73 Dorsal habitus 74 Head and mesosoma, dorsal view 75 Head, anterior view 76 Metasoma and wings, dorsal view.

Material examined. Holotype, female: PAPUA NEW GUINEA: Madang Prov., 100m, 04°16'S 144°58'E, Morox, 1.VIII–18.VIII.2006, yellow pan trap, V. Iwam, OSUC 688076 (deposited in CNCI). *Paratypes*: (21 females, 12 males) INDO-NESIA: 1 female, OSUC 232875 (BPBM). PAPUA NEW GUINEA: 20 females, 12 males, OSUC 232876–232877, 232879–232884, 232886, 232890–232892, 232894–232897 (BPBM); OSUC 688060–688063, 688065–688075, 688077 (CNCI).

Habroteleia scapularis (Kieffer)

http://zoobank.org/6008D3A5-FE3A-4C26-8E5A-455A00D5DB9A http://bioguid.osu.edu/xbiod_concepts/4539

Crestoteleia scapularis Kieffer, 1916: 180 (original description, keyed, spelling error). *Chrestoteleia scapularis* Kieffer: Kieffer 1926: 443, 444 (description, keyed); Baltazar 1966: 182 (cataloged, distribution).

Habroteleia scapularis (Kieffer): Baltazar 1966: 177 (cataloged, generic transfer, distribution); Johnson 1992: 399 (cataloged, type information).

Comments. We were not able to locate the type specimens of this species, and its status and identity are unclear.

Habroteleia soa Chen & Talamas, sp. n.

http://zoobank.org/DD68E31A-9B97-4226-832E-2549DD5F0E0A http://bioguid.osu.edu/xbiod_concepts/448556 Figures 77–81

Description. Body length of female: 3.72 mm (n=1). Length of A3 in male: longer than A2. Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: dense. Sculpture of antennal scrobe: smooth. Central keel: present. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: complete. Sculpture of posterior vertex: punctate rugose. Sculpture of gena: punctate rugose ventrally, sparsely punctate dorsally. Sculpture of occiput: rugulose.

Color of mesosoma: black. Sculpture of dorsal pronotal area: punctate rugose. Sculpture of lateral pronotal area: smooth anteriorly, foveate posteriorly. Sculpture of netrion: coarsely striate. Setae of netrion: sparse throughout. Sculpture of notaulus: contiguously punctate. Sculpture of mesoscutal midlobe: punctate rugose on the anterior margin, otherwise largely smooth with two rows of discrete punctures. Sculpture of lateral lobe of mesoscutum: smooth. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: sparse. Sculpture of mesoscutellum: coarsely punctate rugose. Median propodeal projection: short. Mesopleural carina: weakly developed. Sculpture of mesopleural to mesopleural depression: smooth with a row of punctures along mesopleural carina. Sculpture of dorsal metapleural area: smooth. Sculpture of ventral metapleural area: punctate rugose. Setation of ventral metapleural area: sparse. Color of legs: orange-yellow to dark brown. Sculpture of hind coxa: smooth.

Color of metasoma: black. T1 horn in female: absent. Sculpture of posterior margin of T1 in female: sparsely longitudinally striate. Transverse sulcus on T2: present. Sculpture of T2–T5: T2–T4 sparsely longitudinally striate, with fine punctures in interstices, T5 densely longitudinally striate punctate. Sculpture of T6 in female: densely



Figures 77–81. *Habroteleia soa* sp. n., female, holotype (CASENT 2136859). 77 Lateral habitus 78 Head and mesosoma, lateral view 79 Dorsal habitus 80 Head, anterior view 81 T5 and T6, dorsal view.

punctate. Length of T6 in female: wider than long. Apex of T6 in female: round. Sculpture of S2: longitudinally striate rugose. Sculpture of T1 in male: sparsely longitudinally striate, smooth in interstices. Male T8 apical spine: present.

Etymology. The Malagasy word "soa" means "beautiful" or "excellent". We apply it to this species because we find it to be both of these. The name is treated as a noun in apposition.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=448556]

Material examined. Holotype, female: MADAGASCAR: Antsiranana Auto. Prov., 5km W Manantenina, Camp Mantella, low altitude rainforest, MA-31-32, 490m, 14°26.29'S 49°46.44'E, Marojejy National Park, 14.X–22.X.2005, Malaise trap, M. Irwin & R. Harin'Hala, CASENT 2136859 (deposited in CAS). *Paratypes*: **MADAGASCAR**: 3 males, CASENT 2132434–2132435 (OSUC), 2135976 (CAS).

Comments. *Habroteleia soa* is the most geographically disjunct member of the genus, separated from the other species by the Indian Ocean. Despite this separation, it is not morphologically unusual in comparison with the other species, suggesting either that there is a relatively recent division between *H. soa* and the other species, that the morphology of the genus evolves rather slowly, or that there has been insufficient sampling in the intervening areas (*e.g.*, east Africa, the moist southern part of the Arabian peninsula, India, and all other intervening regions).

Habroteleia spinosa Chen & Johnson, sp. n.

http://zoobank.org/9DD4E72F-B7E1-42CE-95BF-DDA22297830C http://bioguid.osu.edu/xbiod_concepts/448458 Figures 4–5, 82–87

Description. Body length of female: 3.51–3.52 mm (n=2). Body length of male: 3.37–3.81 mm (n=6). Length of A3 in male: longer than A2. Punctation of frons above antennal scrobe: dense. Sculpture of antennal scrobe: punctate rugose. Central keel: present. Sculpture of ventrolateral frons: punctate rugose. Occipital carina: interrupted medially. Sculpture of posterior vertex: smooth with sparse punctures. Sculpture of gena: sparsely punctate. Sculpture of occiput: smooth.

Color of mesosoma: black. Sculpture of dorsal pronotal area: sparsely punctate. Sculpture of lateral pronotal area: largely smooth, with sparsely punctures medially. Sculpture of netrion: coarsely striate ventrally, rugulose dorsally. Setae of netrion: dense throughout. Sculpture of notaulus: discretely punctate. Sculpture of mesoscutal midlobe: densely finely punctate along anterior margin, otherwise smooth. Sculpture of lateral lobe of mesoscutum: smooth. Sculpture of lateral propodeal area: rugose. Setation of mesoscutellum: sparse. Sculpture of mesoscutellum: sparsely punctate. Median propodeal projection: short. Mesopleural carina: distinct. Sculpture of mesepisternum anteroventral to mesopleural depression: smooth. Sculpture of dorsal metapleural area: smooth. Sculpture of ventral metapleural area: rugose. Setation of ventral metapleural area: dense. Color of legs: dark brown to black. Sculpture of hind coxa: smooth.

Color of metasoma: black. T1 horn in female: absent. Sculpture of posterior margin of T1 in female: densely longitudinally striate, punctate rugulose in interstices. Transverse sulcus on T2: present. Sculpture of T2–T5: densely longitudinally striate, punctate rugulose in interstices. Sculpture of T6 in female: rugose. Length of T6 in female: wider than long. Apex of T6 in female: pointed. Sculpture of S2: sparsely longitudinally striate medially, with fine punctures in interstices, irregularly finely punctate laterally. Sculpture of T1 in male: sparsely longitudinally striate, smooth in interstices. Male T8 apical spine: absent.



Figures 82–87. *Habroteleia spinosa* sp. n., female, holotype (OSUC 232889). 82 Lateral habitus 83 Head and mesosoma, lateral view 84 Dorsal habitus 85 Head and mesosoma, dorsal view 86 Head, anterior view 87 Metasoma and wings, dorsal view.

Diagnosis. This species is most similar to *H. salebra* but can be distinguished by the pointed apex of T6 in females and the spine at the apex of T8 in males,

Etymology. The specific epithet means spiny, referring to the pointed apex of T6 in females and should be treated as an adjective.

Link to distribution map. [http://hol.osu.edu/map-large.html?id=448458]

Material examined. Holotype, female: INDONESIA: Papua Prov., W New Guinea Isl., Central Mts., Archbold Lake, 760m, 26.XI-3.XII.1961, sweeping, L.



Figures 88–90. 88 *Habroteleia flavipes*, female (OSUC 688019), T5 and T6, dorsal view. 89–90 *Habroteleia persimilis*, female (OSUC 687934) 89 T5 and T6, dorsal view 90 Wings.

W. Quate, OSUC 232889 (deposited in BPBM). *Paratypes*: (1 female, 6 males) **IN-DONESIA**: 6 males, OSUC 232878, 232887, 232893, 232929–232930, 234491 (BPBM). **PAPUA NEW GUINEA**: 1 female, OSUC 232888 (BPBM).

Acknowledgments

Thanks to L. Musetti and S. Hemly (OSUC) for essential assistance with specimen handling, software, and databasing; Agnièle Touret-Alby (MNHN) and Konstantin Samartsev (ZIN) for imaging type material. We thank the Florida Department of Agriculture and Consumer Services – Division of Plant Industry for their support on this contribution. This material is based upon work supported in part by the National Science Foundation of USA under grant No. DEB-0614764 to N.F. Johnson and A.D. Austin.

References

- Austin AD, Field SA (1997) The ovipositor system of scelionid and platygastrid wasps (Hymenoptera: Platygastroidea): comparative morphology and phylogenetic implications. Invertebrate Taxonomy 11: 1–87. https://doi.org/10.1071/IT95048
- Austin AD, Johnson NF, Dowton M (2005) Systematics, evolution, and biology of scelionid and platygastrid wasps. Annual Review of Entomology 50: 553–582. https://doi. org/10.1146/annurev.ento.50.071803.130500
- Baltazar CR (1961) New generic synonyms in parasitic Hymenoptera. Philippine Journal of Science 90: 391–395.
- Baltazar CR (1966) A catalogue of Philippine Hymenoptera (with a bibliography, 1758–1963). Pacific Insects Monographs 8: 1–488.
- Bin F (1981) Definition of female antennal clava based on its plate sensilla in Hymenoptera Scelionidae Telenominae. Redia 64: 245–261.
- Bin F (1974) The types of Scelionidae [Hymenoptera: Proctotrupoidea] in some Italian collections (Museums of Genoa and Florence, Institute of Portici). Entomophaga 19: 453–466. https://doi.org/10.1007/BF02372781
- Brues CT (1908) Hymenoptera. Fam. Scelionidae. Genera Insectorum 80: 1-59.
- Chen H, Johnson NF, Masner L, Xu Z (2013) The genus *Macroteleia* Westwood (Hymenoptera, Platygastridae s.l., Scelioninae) from China. Zookeys 300: 1–98. https://doi.org/10.3897/ zookeys.313.5106
- Crawford JC (1910) New Hymenoptera from the Philippine Islands. Proceedings of the United States National Museum, 38: 119–133. https://doi.org/10.5479/si.00963801.38-1733.119
- Johnson NF (1992) Catalog of world Proctotrupoidea excluding Platygastridae. Memoirs of the American Entomological Institute 51: 1–825.
- Kelner-Pillault S (1958) Catalogue de quelques types d'Hyménoptères provenant de la collection de l'Abbé J. J. Kieffer. Bulletin du Muséum National d'Histoire Naturelle (2)30: 146–153.
- Kieffer JJ (1905) Nouveaux Proctotrypides exotiques conservés au Musée Civique de Gênes. Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova) 2(2): 9–39.
- Kieffer JJ (1908) Revision des Scelionidae (Hyménoptères). Annales de la Société Scientifique de Bruxelles. Mémoires 32: 111–250.
- Kieffer JJ (1910) Hymenoptera. Fam. Scelionidae. Addenda et corrigenda. Genera Insectorum 80: 61–112.
- Kieffer JJ (1913) Serphides des Îles Philippines. Insecta 3: 253-462.
- Kieffer JJ (1916) Neue Scelioniden aus den Philippinen-Inseln. Brotéria 14: 58–187.
- Kieffer JJ (1926) Scelionidae. Das Tierreich. Vol. 48. Walter de Gruyter & Co., Berlin, 885 pp.
- Kononova SV (1995) [Fam. Scelionidae.] In: Lehr PA (Ed.) [Key to insects of Russian Far East in six volumes. vol. 4. Neuropteroidea, Mecoptera, Hymenoptera. Part 2. Hymenoptera.] Dal'nauka, Vladivostok, 57–121.
- Kononova SV, Kozlov MA (2008) [Scelionids of the Palearctic (Hymenoptera, Scelionidae). Subfamily Scelioninae.] Tovarishchestvo Nauchnykh Izdanii KMK, Saint Petersburg, 489 pp.

- Kononova SV, Petrov S (2000) [A review of the genera *Triteleia*, *Paridris* and *Calotelea* (Hymenoptera, Scelionidae, Scelioninae) of Palaearctic region.] Vestnik Zoologii, 34(6): 27–35.
- Kozlov MA, Kononova SV (1985) [A review of the genera *Triteleia* and *Calliscelio* (Proctotrupoidea, Scelionidae).] Vestnik Zoologii 1985(4): 15–24.
- Kozlov MA, Kononova SV (1990) [Scelioninae of the Fauna of the USSR (Hymenoptera, Scelionidae, Scelioninae).] Nauka, Leningrad, 344 pp.
- Lê XH (2000) Egg-parasites of family Scelionidae (Hymenoptera). Fauna of Vietnam, vol. 3. Science and Technics Publishing House, Hanoi, 386 pp.
- Mani MS, Sharma SK (1982) Proctotrupoidea (Hymenoptera) from India. A review. Oriental Insects 16: 135–258. https://doi.org/10.1080/00305316.1982.10434314
- Masner L (1976) Revisionary notes and keys to world genera of Scelionidae (Hymenoptera: Proctotrupoidea). Memoirs of the Entomological Society of Canada 97: 1–87. https://doi. org/10.4039/entm10897fv
- Masner L (1980) Key to genera of Scelionidae of the Holarctic region, with descriptions of new genera and species (Hymenoptera: Proctotrupoidea). Memoirs of the Entomological Society of Canada 113: 1–54. https://doi.org/10.4039/entm112113fv
- Masner L, Muesebeck CFW (1968) The types of Proctotrupoidea (Hymenoptera) in the United States National Museum. Bulletin of the United States National Museum 270: 1–143. https://doi.org/10.5479/si.03629236.270
- Mikó I, Vilhelmsen L, Johnson NF, Masner L, Pénzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): head and mesosoma. Zootaxa 1571: 1–78.
- Muesebeck CFW, Walkley LM (1956) Type species of the genera and subgenera of parasitic wasps comprising the superfamily Proctotrupoidea (order Hymenoptera). Proceedings of the U.S. National Museum 105: 319–419. https://doi.org/10.5479/si.00963801.3359.319
- Murphy NP, Carey D, Castro LR, Dowton M, Austin AD (2007) Phylogeny of the platygastroid wasps (Hymenoptera) based on sequences from the 18S rRNA, 28S rRNA and cytochrome oxidase *I* genes: implications for the evolution of the ovipositor system and host relationships. Biological Journal of the Linnean Society 91: 653–669. https://doi. org/10.1111/j.1095-8312.2007.00825.x
- Polaszek A, Agosti D, Alonso-Zarazaga M, Beccaloni G, de Place Bjørn P, Bouchet P, Brothers DJ, Earl of Cranbrook, Evenhuis NL, Godfray HCJ, Johnson NF, Krell FT, Lipscomb D, Lyal CHC, Mace GM, Mawatari SF, Miller SE, Minelli A, Morris S, Ng PKL, Patterson DJ, Pyle RL, Robinson N, Rogo L, Taverne J, Thompson FC, van Tol J, Wheeler QD, Wilson EO (2005) A universal register for animal names. Nature 437: 477. https://doi.org/10.1038/437477a
- Saraswat GG, Sharma SK (1978) On some Scelionidae (Hymenoptera: Proctotrupoidea) from India. Memoirs of the School of Entomology, St. John's College, 5: 1–46.
- Sharma SK (1981) First record of *Triteleia* Kieffer (Hymenoptera: Proctotrupoidea: Scelionidae) from India with descriptions of two new species. Oriental Insects 14: 447–451. https://doi.org/10.1080/00305316.1980.10434830
- Talamas EJ, Pham H-T (2017) An online photographic catalog of Platygastroidea (Hymenoptera) in the Institute of Ecology and Biological Resources (Hanoi, Vietnam), with some taxonomic notes. Journal of Hymenoptera Research 56: 225–239. https://doi. org/10.3897/jhr.56.10214

- Talamas EJ, Thompson J, Cutler A, Fitzsimmons Schoenberger S, Cuminale A, Jung T, Johnson NF, Valerio AA, Smith AB, Haltermann V, Alvarez E, Schwantes C, Blewer C, Bodenreider C, Salzberg A, Luo P, Meislin D, Buffington ML (2017) An online photographic catalog of primary types of Platygastroidea (Hymenoptera) in the National Museum of Natural History, Smithsonian Institution. Journal of Hymenoptera Research 56: 187–224. https://doi.org/10.3897/jhr.56.10774
- Vilhelmsen L, Mikó I, Krogmann L (2010) Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insects: Hymenoptera). Zoological Journal of the Linnean Society 159: 22-194. https://doi.org/10.1111/j.1096-3642.2009.00576.x
- Yoder MJ, Mikó I, Seltmann K, Bertone MA, Deans AR (2010) A gross anatomy ontology for Hymenoptera. PLos ONE 5(12): e15991. https://doi.org/10.1371/journal.pone.0015991

Appendix I

eye

femur

frons

gena head

fore wing

dpa

Ontolog	y database.	
	A1	http://purl.obolibrary.org/obo/HAO_0000908
	A2	http://purl.obolibrary.org/obo/HAO_0000706
	A3	http://purl.obolibrary.org/obo/HAO_0001148
	A7	http://purl.obolibrary.org/obo/HAO_0001885
	A12	http://purl.obolibrary.org/obo/HAO_0001884
	antenna	http://purl.obolibrary.org/obo/HAO_0000101
	antennomere	http://purl.obolibrary.org/obo/HAO_0000107
	area	http://purl.obolibrary.org/obo/HAO_0000146
	body	http://purl.obolibrary.org/obo/HAO_0000182
	carina	http://purl.obolibrary.org/obo/HAO_0000188
	central keel	http://purl.obolibrary.org/obo/HAO_0000109
сра	cervical pronotal area	http://purl.obolibrary.org/obo/HAO_0000194
	clava	http://purl.obolibrary.org/obo/HAO_0000203
	clypeus	http://purl.obolibrary.org/obo/HAO_0000212
	compound eye	http://purl.obolibrary.org/obo/HAO_0000217
	соха	http://purl.obolibrary.org/obo/HAO_0000228
	depression	http://purl.obolibrary.org/obo/HAO_0000241
	dorsal pronotal area	http://purl.obolibrary.org/obo/HAO_0000267
	egg	http://purl.obolibrary.org/obo/HAO_0000286
	epomial carina	http://purl.obolibrary.org/obo/HAO_0000307

http://purl.obolibrary.org/obo/HAO_0000217

http://purl.obolibrary.org/obo/HAO_0000327

http://purl.obolibrary.org/obo/HAO_0000351

http://purl.obolibrary.org/obo/HAO_0001523 http://purl.obolibrary.org/obo/HAO_0000371

http://purl.obolibrary.org/obo/HAO_0000397

Table I. URI Table matching terms and concepts used in this revision with the Hymenoptera Anatomy

	hind coxa	http://purl.obolibrary.org/obo/HAO_0000587
	hind tibia	http://purl.obolibrary.org/obo/HAO_0000631
	hind wing	http://purl.obolibrary.org/obo/HAO_0000400
dpa	inner orbit	http://purl.obolibrary.org/obo/HAO_0000419
-	interantennal process	http://purl.obolibrary.org/obo/HAO_0000422
	lateral lobe of mesoscutum	http://purl.obolibrary.org/obo/HAO_0000466
	lateral ocellus	http://purl.obolibrary.org/obo/HAO_0000481
LOL	lateral ocellar line	http://purl.obolibrary.org/obo/HAO_0000480
	lateral pronotal area	http://purl.obolibrary.org/obo/HAO_0000483
	malar sulcus	http://purl.obolibrary.org/obo/HAO_0000504
lpa	mandible	http://purl.obolibrary.org/obo/HAO_0000506
	margin	http://purl.obolibrary.org/obo/HAO_0000510
	mesepisternum	http://purl.obolibrary.org/obo/HAO_0001872
	mesopleural depression	http://purl.obolibrary.org/obo/HAO_0000326
	mesopleuron	http://purl.obolibrary.org/obo/HAO_0000566
	mesoscutellum	http://purl.obolibrary.org/obo/HAO_0000574
	mesoscutum	http://purl.obolibrary.org/obo/HAO_0001490
	mesosoma	http://purl.obolibrary.org/obo/HAO_0000576
	metapleuron	http://purl.obolibrary.org/obo/HAO_0000621
med	metascutellum	http://purl.obolibrary.org/obo/HAO_0000625
	metasoma	http://purl.obolibrary.org/obo/HAO_0000626
	mesoscal midlobe	http://purl.obolibrary.org/obo/HAO_0000520
	netrion	http://purl.obolibrary.org/obo/HAO_0000644
	notauli (notaulus)	http://purl.obolibrary.org/obo/HAO_0000647
	occipital carina	http://purl.obolibrary.org/obo/HAO_0000653
	ocellus	http://purl.obolibrary.org/obo/HAO_0000661
ot	ocellar triangle	http://purl.obolibrary.org/obo/HAO_0000430
0.01	ocular ocellar line	http://purl.obolibrary.org/obo/HAO_0000662
OOL	orbit	http://purl.obolibrary.org/obo/HAO_0000672
	posterior ocellar line	http://purl.obolibrary.org/obo/HAO_0000759
	process	http://purl.obolibrary.org/obo/HAO_0000822
	propodeum	http://purl.obolibrary.org/obo/HAO_0001248
	S1	http://purl.obolibrary.org/obo/HAO_0001997
	S2	http://purl.obolibrary.org/obo/HAO_0001829
	\$3	http://purl.obolibrary.org/obo/HAO_0001831
	<u>S4</u>	http://purl.obolibrary.org/obo/HAO_0001832
	\$5	http://purl.obolibrary.org/obo/HAO_0001833
POL	<u>\$6</u>	http://purl.obolibrary.org/obo/HAO_0001834
	S7	http://purl.obolibrary.org/obo/HAO_0002185
	sculpture	http://purl.obolibrary.org/obo/HAO_0000913
	sternite	http://purl.obolibrary.org/obo/HAO_0001654
	sulcus	http://purl.obolibrary.org/obo/HAO_0000978
	T1	http://purl.obolibrary.org/obo/HAO_0000053
	T2	http://purl.obolibrary.org/obo/HAO_0000056
	Т3	http://purl.obolibrary.org/obo/HAO_0000057
	T4	http://purl.obolibrary.org/obo/HAO_0000058

	T5	http://purl.obolibrary.org/obo/HAO_0000059
	Т6	http://purl.obolibrary.org/obo/HAO_0000060
	T7	http://purl.obolibrary.org/obo/HAO_0000061
	tergite	http://purl.obolibrary.org/obo/HAO_0001783
DOI	tibia	http://purl.obolibrary.org/obo/HAO_0001017
POL	tyloid	http://purl.obolibrary.org/obo/HAO_0001199
	vein	http://purl.obolibrary.org/obo/HAO_0001095
	vertex	http://purl.obolibrary.org/obo/HAO_0001077
	vertical epomial carina	http://purl.obolibrary.org/obo/HAO_0000307
	wing	http://purl.obolibrary.org/obo/HAO_0001089

RESEARCH ARTICLE



Ten unique and charismatic new species of Microgastrinae wasps (Hymenoptera, Braconidae) from North America

Jose Fernandez-Triana¹

I Canadian National Collection of Insects, Ottawa, Canada

Corresponding author: Jose Fernandez-Triana (jose.fernandez@agr.gc.ca)

Academic editor: K. van Achterberg Received 8 December 2017 Accepted 13 January 2018 Published 18 January 201
http://zoobank.org/16CAB66E-F256-4232-9017-110246C3CCFC

Citation: Fernandez-Triana J (2018) Ten unique and charismatic new species of Microgastrinae wasps (Hymenoptera, Braconidae) from North America. ZooKeys 730: 123–150. https://doi.org/10.3897/zookeys.730.22869

Abstract

Ten new species within four genera of Microgastrinae parasitoid wasps (Hymenoptera: Braconidae) are described from Canada and United States: *Diolcogaster ichiroi*, *Diolcogaster miamensis*, *Glyptapanteles pseudotsugae*, *Microgaster archboldensis*, *Microgaster syntopic*, *Microplitis altissimus*, *Microplitis jorgeluisi*, *Microplitis julioalbertoi*, and *Microplitis mariamargaritae*. The new taxa are significant because they represent the first North American records of a tropical group (species of the *basimacula* group in *Diolcogaster*), exemplify interesting ecological cases (niche-based host selection in *Glyptapanteles*, syntopic species in *Microgaster*), and showcase unique morphological features and/or altitudinal records (*Microplitis*). Most of the new species were collected in protected areas or areas with strong research programs (Archbold Biological Station and hammock forests near Miami, Florida; Great Sand Dunes National Park and Preserve, and Mount Evans Wilderness Area, Colorado; Sapelo Island, Georgia; Tonto National Forest, Arizona), and thus are also of value and interest for conservation and research efforts.

Keywords

Microgastrinae, North America, conservation, species diversity, parasitoid wasps

Introduction

Microgastrine wasps are the second largest subfamily of Braconidae (Hymenoptera) with 2,700+ described species and an estimate 17,000-46,000+ worldwide (Rodriguez et al. 2013, Yu et al. 2016). It is also one of the most important groups in the biological control of agricultural and forestry pests worldwide (Whitfield 1997).

The Nearctic region (Canada, Greenland, and United States) has historically been considered as one of the best studied and best known natural regions of the planet. However, regarding microgastrine wasps that has not been the case: of the six major biogeographical regions considered in the 2016 version of Taxapad (Yu et al. 2016) the Nearctic is the second least diverse at species level, only surpassing the Australasian region. There are currently 330 described species of Microgastrinae in North America, and the progress has been relatively slow compared to other regions of the planet. After two seminal works from Muesebeck (1921, 1922), most of the new taxa recorded for the Nearctic have been described in papers dealing with single species, usually of interest in biological control (see references in Yu et al. 2016), with only few recent papers describing more than one species (e.g., Whitfield 1985, 2006, Williams 1981, 1988, Valerio et al. 2009, Fernandez-Triana 2010, Valerio and Whitfield 2015).

Hundreds of additional species for this region have been revealed by DNA barcoding (e.g., Smith et al. 2013), but the west coast and southernmost areas of North America, which also happen to be the most diverse, have barely been analyzed, suggesting that the actual species diversity in the region will be several times higher –when more studies are done.

To highlight how few we currently know about the group in the region, we describe below ten new species within four genera of Microgastrinae. All of the new species represent significant and in many cases unique records, as this paper intends to bring further attention to special conservation areas in North America.

Methods

All specimens studied for this paper are deposited in the Canadian National Collection of Insects, Ottawa (CNC).

Morphological terms and measurements of structures follow those used by Mason (1981), Huber and Sharkey (1993), Whitfield (1997), Karlsson and Ronquist (2012), and Fernandez-Triana et al. (2014).

The abbreviations T1, T2, and T3 refer to metasomal mediotergites 1, 2, 3; F2/3/14/15/16 refer to length of antennal flagellomeres 2, 3, 14, 15 and 16; and L and W refer to length and width respectively. The description of the new species contains some ratios commonly used in taxonomic studies of Microgastrinae, but raw measurements of morphological structures (in mm) are also provided as they allow for additional ratios to be explored in the future, if needed. When presenting the raw measurements, the holotype value is given first, followed by the range of other specimens between parentheses.

For some specimens DNA barcodes (the 5' region of the cytochrome c oxidase

I (CO1) gene, Hebert et al. 2003) were available. DNA extracts were obtained from single legs using a glass fibre protocol (Ivanova et al. 2006). Total genomic DNA was re-suspended in 30 μ l of dH2O, a 658-bp region near the 5' terminus of the CO1 gene was amplified using standard primers (LepF1–LepR1) following established protocols (http://v4.boldsystems.org/index.php), and a composite sequence was generated for all successful amplifications. All information for the sequences associated with each individual specimen can be retrieved from the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007).

Photos were taken with a Keyence VHX-1000 Digital Microscope, using a lens with a range of $10-130 \times$. Multiple images were taken of a structure through the focal plane and then combined to produce a single in-focus image using the software associated with the Keyence System. Plates were prepared using Microsoft PowerPoint 2010.

A map with the distribution of the species was generated using SimpleMappr (Shorthouse 2010).

For states of the United States and for Canadian provinces/territories, acronyms consisting of two capital letters are used, following Canada Post (http://www.canada-post.ca/tools/pg/manual/PGaddress-e.asp).

Results

Ten new Nearctic species of Microgastrinae are described below, arranged alphabetically by genus (and species within every genus). Every new species is compared and diagnosed against all other previously described Nearctic species of that genus. The new taxa are significant because they represent the first North American records of a tropical group (species of the *basimacula* group in *Diolcogaster*), exemplify interesting ecological cases (niche-based host selection in *Glyptapanteles*, syntopic species in *Microgaster*), and showcase unique morphological features and/or altitudinal records (*Microplitis*).

Four of the described species were found in south Florida, three were found in the mountains of Colorado, and another two species were distributed across the west coast of North America (Figure 11). In most cases, the new species were collected or reared in protected areas and/or areas with strong research programs (Archbold Biological Station and hammock forests near Miami, FL; Great Sand Dunes National Park and Preserve, and Mount Evans Wilderness Area, CO; Sapelo Island, GA; Tonto National Forest, AZ), and thus by describing them it is hoped further attention is brought into their conservation.

Genus Diolcogaster Ashmead, 1900

There are nine described species of *Diolcogaster* in the Nearctic (Yu et al. 2016), but many more await description. The two new species described below are very distinct

from any previously described species in North America, as they both belong to the *basimacula* species-group, a mostly a tropical group, with dozens of undescribed species worldwide. The finding of these species in mainland North America is unique, but not entirely surprising as south Florida has close biogeographical affinities with the Neotropical fauna (e.g., Snyder et al. 1990). The description of these two new species will hopefully bring further attention to the unique values of the biodiversity in south Florida and the need to preserve those ecosystems.

Diolcogaster ichiroi Fernandez-Triana, sp. n.

http://zoobank.org/717E90BC-7742-4D0D-80B9-9A4FD5998D82 Fig. 1

Holotype. Female, CNC, UNITED STATES. Holotype locality: Archbold Biological Station, Highlands County, Florida, USA.

Holotype labels. First label: USA: FL, Highlands Co./Archbold Biol. Sta./1–8. vi.1987/Dr.X.Wahl. Second label: CNC483614.

Paratypes. 2♀, 5 ♂ (CNC) from the same locality than holotype. Voucher codes: CNC483650–CNC483652, CNC489768, CNC489820, CNC489849, CNC526748. Collecting dates: 1-22.vii.1987 and 18.iii-4.iv.1988, some specimens collected with a Malaise trap.

Diagnosis. *Diolcogaster ichiroi* and *D. miamensis* (see next species below) are very distinct and unique among all known species of *Diolcogaster* from North America, based on its tergites 1–3 forming a carapace that covers most of the metasoma. That is the main distinguishing feature of the *basimacula* group, which is very speciose in the Old World tropics but until now had never been reported from the New World (al-though numerous undescribed species from the Neotropics are found in collections). *Diolcogaster ichiroi* (body mostly yellow, with some small brown areas; fore wing centrally with some veins transparent) has different coloration than *D. miamensis* (head yellow frontally, orange in the back; meso- and metasoma mostly black; fore wing centrally with veins brown); the two species also differ in the shape and sculpture of T2 (anterior and posterior margin of T2 more or less straight in *ichiroi*, curved in *miamensis*, compare Figs 1D, 2F), as well as setae thickness near apex of ovipositor sheaths (all setae of same thickness in *miamensis*, a couple of setae thicker than the rest in *ichiroi*).

Description. Female. Body color mostly yellow (with some brown spots on metasoma; T4+ dark brown; anterior laterotergies and sternites, pro- and mesocoxae, all trochanters and trochantellus, anterior 0.2–0.3 of tibiae, and metatibial spurs white; antenna flagellomeres mostly yellow, but with tip brown. Wings mostly hyaline but with a couple of infumate spots, some veins brown and some transparent, pterostigma brown. Body mostly coarsely sculptured. Scutoscutellar sulcus with 9–10 costulae. Hind wing with vannal lobe straight to slightly concave and centrally without setae. Tarsal claws simple. T1–3 forming a carapace that covers most of metasoma, T4+ scarsely visible. Ovipositor sheaths relatively short, with long setae, including a cou-



Figures I. Diolcogaster ichiroi, female holotype.

ple of thicker setae near apex of sheaths. **Body measurements (mm).** Body L: 2.3 (2.0–2.1); fore wing L: 2.1 (1.8–2.0); ovipositor sheaths L (approximate measurement): 0.12 (0.11); metafemur L/W: 0.65/0.18 (0.65/0.18); metatibia L: 0.81 (0.81); metatibia inner/outer spurs L: 0.21/0.16 (0.21/0.15); first segment of metatarsus L:

0.38 (0.37); F2/3/14/15/16: 0.19/0.17/0.09/0.09/0.11 (0.20/0.17/0.09/0.09/0.11); ocular–ocellar line: 0.10 (0.10); interocellar distance: 0.10 (0.11); posterior ocellus diameter: 0.06 (0.07).

Male. As female, but darker (more extensive brown areas on anteromesoscutum, mesoscutellar-axillar complex, metascutellum and metasomal terga).

Distribution. United States: FL. Only known from the type locality (Archbold Biological Station).

Etymology. This unique and remarkable species is named to honor the truly unique and remarkable Ichiro Suzuki, my favorite baseball player and one the best ever to play the game. At the time the research for this paper was being conducted, Ichiro was still playing for a Florida team and thus naming a species endemic from Florida after him made complete sense. Unfortunately, the new owners of the Miami Marlins did not keep Ichiro, an unpopular decision not liked by many Marlins fans. Hopefully soon another Major League team gives the Universal Hit King the chance to continue his extraordinary career in baseball.

Notes. Both this species and the next one are examples of mostly tropical groups that in North America are only found in south Florida (e.g., Snyder et al. 1990). Altogether with other microgastrine wasps recently described from that area (see Fernandez-Triana and Boudreault 2016, as well as the two new *Microgaster* species being described below in this paper), all of these taxa highlight the importance of biodiversity studies in south Florida and the need to increase conservation efforts there.

Diolcogaster miamensis Fernandez-Triana, sp. n.

http://zoobank.org/85DAD587-5462-46E7-A8AE-1138554AE4F0 Fig. 2

Holotype. Female, CNC, UNITED STATES. Holotype locality: Hammock forest on Chekika State Park Recreation Area, SW of Miami, Dade County, Florida, USA.

Holotype labels. First label: FLA: Dade Co; Chekika St./Rec. Area, 50 km SW Miami/1.v–2.viii.1985, S&J Peck/Grossman Hammock For./malaise-FIT. Second label: CNC735735.

Paratypes. 1 ♂ (CNC) from Archbold Biological Station, Highlands County, Florida, USA. Voucher code: CNC489838. Collecting dates: 18–22.iii.1987.

Diagnosis. See *Diolcogaster ichiroi* above for details on how these two species are distinct from each other and from all other known *Diolcogaster* in North America.

Description. Female. Body coloration varied: head yellow frontally, orange in the back, antenna flagellomeres mostly yellow, but with tip brown; meso- and metasoma mostly black, with some small areas light brown; legs mostly yellow-white, with most of metafemur and posterior 0.5 of metatibia brown, and metatarsus yellow-brown. Wings mostly hyaline, with slightly infumate spot below pterostigma, most veins brown and pterostigma brown. Body mostly coarsely sculptured. Scutoscutellar sulcus with 8 costulae. Hind wing with vannal lobe straight to slightly concave and centrally



Figures 2. Diolcogaster miamensis, male paratype.

without setae. Tarsal claws simple. T1–3 forming a carapace that covers rest of metasoma. Ovipositor sheaths relatively short, with long setae (but all of same thickness). **Body measurements (mm).** Body L: 2.2; fore wing L: 2.2; ovipositor sheaths L (approximate measurement): 0.15; metafemur L/W: 0.68/0.22; metatibia L: 0.87; metatibia inner/outer spurs L: 0.27/0.20; first segment of metatarsus L: 0.41; F2/3/14/15/16: 0.23/0.21/0.12/0.11/0.14; ocular–ocellar line: 0.09; interocellar distance: 0.08; posterior ocellus diameter: 0.07.

Male. As female.

Distribution. United States: FL. Only known from two localities in south Florida.

Etymology. Named after the Miami metropolitan area (also known as Greater Miami or South Florida), where the holotype locality is found, to highlight the great natural values of the area and to bring further attention to the conservation and appreciation of nature in south Florida.

Notes. See Notes above (under *Diolcogaster ichiroi*) for more details on the conservation value of these species. Both specimens of *D. miamensis* were collected with Malaise traps.

Genus Glyptapanteles Ashmead, 1904

There are 18 described species of *Glyptapanteles* in the Nearctic (Yu et al. 2016), but many more await description. The new species described below is very distinctive because on its enlarged eyes, the first North American species of the genus with that character. A related genus, *Distatrix*, shares this feature, but the new species clearly belongs to *Glyptapanteles* due to the presence of two pronotal furrows (*Distatrix* only has one pronotal furrow, see Mason 1981) and the host families it parasitizes. From a biological perspective, the new species is also unique, as it parasitizes different host caterpillars feeding on Douglas fir across a range of 2,500 km in western North America.

Glyptapanteles pseudotsugae Fernandez-Triana, sp. n.

http://zoobank.org/58D06EA4-35DE-4D8B-91D1-E2F897D8EA87 Fig. 3

Holotype. Female, CNC, UNITED STATES. Holotype locality: Aztec Peak, Arizona, USA.

Holotype labels. First label: Aztek Pk., AR./coll. vi-1-77/em. vi-24/Torg. 1977 7065A. Second label: Ex *Orgya pseudotsugata*. Third label: Hopk. US/65254. Fourth label: CNC666525.

Paratypes. 11 \bigcirc , 17 \checkmark (CNC) from the following localities. Canada: AB, Pincher Creek; BC, Carquile; BC, Elko; BC, Mount Lolo; BC, Nelson; BC, Lake Williams. United States: AZ, Aztec Peak, Tonto National Forest; CA, El Dorado County, Iron Mountain; CA, San Bernardino County, Sky Forest; CA, Stowe Reservoir; CA, Modoc County, Tom's Creek; OR, Chiloquin Ridge; OR, Forth Klamath. Voucher codes: CNC841809– CNC841836. All of the specimens were reared, with emergence dates from early June to early August.



Figures 3. *Glyptapanteles pseudotsugae*, female holotype.

Diagnosis. The enlarged eyes and ocelli of *G. pseudotsugae* are unlike those of any other described species of *Glyptapanteles* in North America –all of which have normal-sized eyes. The antenna of females is also rather long, with the last flagellomeres not significantly reduced, as it is the case with most Microgastrinae female specimens. The size of eyes and ocelli, the relatively long antenna, and the yellow-brown body coloration are all morphological features that strongly suggest this species is nocturnal or crepuscular – see Quicke (2015) for a summary and further references on the suite of characters that are typical of nocturnal/crepuscular parasitoid wasps. The caterpillar hosts are also unique among known hosts of Microgastrinae (see below).

Description. Female. Body mostly brown to dark brown (except for yellow scape, pedicel, labrum, mandibles, palpi, tegula; humeral complex half yellow and half brown; T3+ partially yellow; anterior laterotergites and sternites mostly yellow; hypopygium sometimes partially yellow); most of legs yellow, but metacoxa, apical 0.1 of metafemur and metatibia, and metatarsus brown. Wings hyaline, pterostigma brown, veins mostly transparent (except for a few veins closer to pterostigma). Body mostly smooth and shiny, at most with fine, shallow and sparse punctures; propodeum with small striae around nucha; apical 0.3 of T1 and most of T2 (except centrally) with relatively coarse longitudinal striation. Head with eyes and ocelli enlarged. Protarsus with a thick and curved seta. Fore wing with veins r and 2RS meeting at a sharp angle, with vein 3RSa being a very small stub; vein R1 longer than pterostigma. Legs with tarsal claws simple. T1 narrowing towards posterior margin, T2 subtriangular (trapezoidal). Ovipositor sheaths with a few, large setae near tip. **Body measurements (mm).** Body L: 3.3 (3.2-3.7); fore wing L: 3.6 (3.7-4.1); ovipositor sheaths L: 0.15-0.20 (approximate measurement); metafemur L/W: 1.02/0.25 (1.04/0.25); metatibia L: 1.18 (1.22-1.24); metatibia inner/outer spurs L: 0.33/0.26 (0.32-0.36/0.24-0.26); first segment of metatarsus L: 0.48 (0.50-0.55); F2/3/14/15/16: 0.32/0.30/0.15/0.14/0.16 (0.31-0.32/0.29-0.30/0.14-0.15/0.13/0.15-0.16; ocular-ocellar line: 0.06 (0.04-0.07); interocellar distance: 0.12 (0.10–0.13); posterior ocellus diameter: 0.11 (0.11–0.12).

Male. As female, but eyes not enlarged, and general coloration, especially on metasoma, darker.

Variation. Compared to the US specimens, the Canadian specimens are darker (dark brown to black scape, clypeus, labrum and most tergites) and also slightly larger (0.1–0.2 mm longer wings and body).

Distribution. Western North America, from 33°–52°N. Canada: AB, BC. United States: AZ, CA, OR.

Host data. The US specimens of *Glyptapanteles pseudotsugae* were all reared from the Douglas-fir tussock moth, *Orgya pseudotsugata* (McDunnough, 1921) (Lymantriidae), while the Canadian specimens were reared from three different species of Geometridae: the Spruce-fir looper *Macaria signaria dispuncta* (Walker, 1860), the Brownlined looper *Neoalcis californiaria* (Packard, 1871), and *Pero behrensarius behrensarius* (Packard, 1871). Most of the specimens we examined had remnants of the host larva and/or the wasp cocoon preserved (kept in a gel capsule, pinned or glued to the paper where the adult wasp was mounted); based on that evidence, the parasitoid is con-

sidered to be solitary. *Glyptapanteles pseudotsugae* is the first species of Microgastrinae recorded attacking those four species of Lepidoptera. [There actually is an earlier mention of this wasp species, as an unidentified "*Apanteles* sp.", in a previous publication studying the parasitoids and predators of *Orgya pseudotsugata* (Dahlsten et al. 1977); that is to be expected as all *Glyptapanteles* species were considered to belong to *Apanteles* until Mason (1981) split the latter genus into several]. The four lepidopteran hosts recorded above all feed on Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco.

Etymology. Named after the genus name of the Douglas fir, *Pseudotsuga*, as that plant harbours all caterpillar species that are host of the parasitoid wasp in North America.

Notes. *Glyptapanteles pseudotsugae* is an example of niche-based selection of caterpillar hosts by a parasitoid wasp, as all of the Lepidoptera species recorded here coexist on fir forests in North America (e.g., Mason 1987). That contrasts with the recorded information for most Microgastrinae wasps, which usually parasitize taxonomically related hosts. Despite the relatively wide geographical distribution of the species in western North America (the distance between the southernmost known specimens in central Arizona and the northernmost known specimens in southern British Columbia is approximately 2,500 km), and the different hosts species parasitized across the wasp range, only minor morphological differences are apparent, and thus the US and Canadian wasp specimens are here considered to be conspecific. Many of the US specimens from the type series detailed above come from Dahlsten et al. (1977), although those authors saw additional specimens not seen nor studied for this paper. No molecular data is known for this species.

Genus Microgaster Latreille, 1804

There are 18 described species of *Microgaster* in the Nearctic (Yu et al. 2016), with many more undescribed. The two new species described below are very distinctive because of their large body size and characteristic color patterns, as well as the arrangement of placodes on the antennal flagellomeres, unique among all other known species of the genus in North America. Based on the strong morphological similarities and the shared geographic distribution (at least partially), they very likely represent an example of sympatric speciation. Furthermore, both new species were mostly found in important conservation areas of south Florida and Georgia; its description also intends to increase public awareness of the biodiversity values of those areas.

Microgaster archboldensis Fernandez-Triana, sp. n. http://zoobank.org/C115F955-C73A-4B06-8EB1-BA0292977DAD Fig. 4

Holotype. Female, CNC, UNITED STATES. Holotype locality: Archbold Biological Station, Highlands County, Florida, USA.



Figures 4. Microgaster archboldensis, female holotype.

Holotype labels. First label: U.S.A. FL: Highlands Co./Archbold Biol. Sta./1-8. vi.1987, D. B. Wahl/CNC489773.

Paratypes. 1♀, 8 ♂ (CNC) from the same locality than holotype. Voucher codes: CNCHYM 01662, CNCHYM 01663, CNCHYM 01665, CNC483424, CNC489814,

CNC654633–CNC654636. Collecting dates: 1–29.vi.1987 and 18–24.viii.1987, some specimens collected with Malaise trap and others with flight interception traps.

Diagnosis. Microgaster archboldensis and M. syntopic are very distinct and unique among all known species of Microgaster from North America because of its color pattern, body size, and flagellomeres with three rows of placodes. The latter is the most important feature, as it had not been recorded from any known Nearctic species until now, and it was rather considered to characterize the different but related genus Hygroplitis (e.g., Mason 1981). However, M. archboldensis and M. syntopic clearly belong to Microgaster as they both have pectinated tarsal claws, pleated hypopygium, apical tarsomeres not enlarged, and body not partially depressed (whereas Hygroplitis has simple tarsal claws, inflexible hypopygium, apical tarsomeres enlarged and body partially depressed). Besides morphology, available DNA barcodes clearly place these new species within Microgaster and not Hygroplitis. Microgaster archboldensis can in turn be separated from M. syntopic because of different color of front and mid legs, part of propodeum, scutellar disc and metanotum (compare Figs 4A, C, F versus Figs 5A, C, E); longer ovipositor sheaths, body length and fore wing length; and some additional minor differences in mesopleuron sculpture, and number of costulae in scutoscutellar sulcus. From a molecular perspective (DNA barcoding), the two species differ in 27 base pairs (bp), which amounts to a rather significant difference of more than 4.5% bp (the available sequences for *M. archboldensis* represent almost complete barcodes with 626-627 bp, but the available sequences for *M. syntopic* are shorter at only 422–593 bp).

Description. Female. Head and mesosoma mostly black (except for reddish-orange spots on posterior half of propodeum, posterior margin of scutellar disc and central part of metanotum); metasoma with T1–3 reddish-orange, T4+ orange-yellow, hypopygium mostly yellow to yellow-white; front legs entirely dark brown to black; mid legs almost entirely dark brown to black (except for coxa, trochanter and trochantellus, which are partially orange and partially dark brown); hind legs mostly orange (except for posterior 0.3 of metatibia, metatibial spurs and metatarsus which are dark brown to black); wings strongly infumated, pterostigma and veins dark brown to black. Flagellomere with three rows of placodes. Scutoscutellar sulcus with 5–6 costulae. Hypopygium pleated. Tarsal claws pectinate. **Body measurements (mm)**. Body L: 5.2 (5.4); fore wing L: 5.3 (5.5); ovipositor sheaths L: 1.28 (1.30); metafemur L/W: 1.64/0.51 (1.70/0.54); metatibia L: 1.96 (2.02); metatibia inner/outer spurs L: 0.76/0.47 (0.76/0.51); first metatarsus segment L: 0.97 (0.96); F1/2/3/14/15/16: 0.40/0.41/0.42/0.21/0.18/0.20 (0.40/0.43/0.43/0.24/0.20/0.21).

Male. As female.

Molecular data. Three barcode-compliant sequences, representing BIN BOLD:AAZ7880 in BOLD.

Distribution. United States: FL. Only known from the type locality, Archbold Biological Station.

Etymology. Named after the Archbold Biological Station in Florida, US, to recognize the extraordinary fauna of Microgastrinae (and certainly of many other taxa) that it harbors and protects. **Notes.** In spite of the relatively strong morphological and molecular differences, *Microgaster archboldensis* still seems very close to *M. syntopic*, and both are at least partially sympatric in central Florida. See Notes above (under *Diolcogaster ichiroi*) for more details on the conservation value of all these species.

Microgaster syntopic Fernandez-Triana, sp. n. http://zoobank.org/8F6554C3-FEE9-40D9-ADC7-414E4A9C1990 Fig. 5

Holotype. Female, CNC, UNITED STATES. Holotype locality: Archbold Biological Station, Highlands County, Florida, USA.

Holotype labels. First label: USA: FL, Highland Co./ Lake Placid/ Archibold Biol. Sta./ 8-14.ix.1987; FIT/ BRC HYMN TEAM. Second label: CNC483215.

Paratypes. $2\bigcirc$, $5 \circlearrowright$ (CNC) from the same locality than holotype, collecting dates: 26.iv.1967, 23.v.1967, 1–8.vi.1987, 9–22.vi.1987, 21.ix.1987; $3\bigcirc$, $2 \circlearrowright$ (CNC) from USA, FL, Alachua County, Gainesville, American Entomological Institute, collecting dates: 1–15.ix.1987, 29.ix.1986, 6.x.1986, 24.vi–13.viii.1987; $4 \diamondsuit$ (CNC) USA, GA, McIntosh County, Sapelo Island, Oak forest, collecting dates: 20.vi–18.vii.1987, 15.vii-9.ix.1987. Voucher codes: CNCHYM 01664, CNCHYM 07428, CNCHYM 07429, CNC280981, CNC280993, CNC280996, CNC483414, CNC483415, CNC483419, CNC483355, CNC489769, CNC489772, CNC489778, CNC841837–CNC841839. Some specimens were collected with Malaise trap and others with flight interception traps.

Diagnosis. See *Microgaster archboldensis* above for details on how these two species are distinct from each other and from all other known *Microgaster* in North America.

Description. Female. Head and mesosoma black; metasoma with T1–3 reddish-orange, T4+ and hypopygium orange-yellow; all legs mostly reddish-orange (except for posterior 0.2–0.1 of metatibia, metatibial spurs and metatarsus which are dark brown to black); wings strongly infumated, pterostigma and veins dark brown to black. Flagellomere with three rows of placodes. Scutoscutellar sulcus usually with 7–8 costulae (rarely with 5–6). Hypopygium pleated. Tarsal claws pectinate. **Body measurements (mm).** Body L: 4.6 (4.6–5.2); fore wing L: 4.9 (4.8–5.3); ovipositor sheaths L: 0.85 (0.86–0.94); metafemur L/W: 1.56/0.46 (1.50–1.63/0.50–0.54); metatibia L: 1.82 (1.82–1.98); metatibia inner/outer spurs L: 0.66/0.41 (0.70–0.78/0.46–0.50); first metatarsus segment L: 0.83 (0.80–0.98); F1/2/3/14/15/16: 0.40/0.40/0.40/0.19/0.18/0.20 (0.38–0.43/0.39–0.45/0.40– 0.44/0.19–0.20/0.16/0.19–0.20).

Male. As female.

Molecular data. Two sequences, one of them barcode-compliant, representing BIN BOLD:AAZ7881 in BOLD.

Distribution. United States: FL, GA. Only known from two localities in Florida and one in Georgia.



Figures 5. Microgaster syntopic, female holotype.

Etymology. Derived from Greek, 'syntopic' meaning 'from the same place', a term used in Zoology to reference two or more related species which can occupy the same locality/ habitat, and could possibly hybridize or even be sister species (see explanation of the concept in Rivas 1964). The name refers to this species being syntopic with *Microgaster archboldensis*

(at least around Archbold Biological Station, where both species were collected, sometimes on the same date and by the same Malaise trap).

Notes. See Notes above (under *Diolcogaster ichiroi*) for more details on the conservation value of these species.

Genus Microplitis Foerster, 1863

There are 36 described species of *Microplitis* in the Nearctic (Yu et al. 2016), but many more remain undescribed in the region (e.g., Fernandez-Triana 2010). The five new species described below are very distinctive on different accounts (relatively large or small body size, extremely long metasoma, unique hypopygium and/or ovipositor sheath shapes, wing coloration, elongated mouth parts). One of the new species represents the highest altitude record of a microgastrine wasp ever reported in North America (and indeed one of the highest ever recorded for that group in the world). Another new species has the longest metasoma ever observed in the Microgastrinae subfamily. In all cases, most of the specimens were collected in protected or significant areas. Their description intend to bring further appreciation of the extraordinary diversity and uniqueness of parasitoid wasps.

Microplitis altissimus Fernandez-Triana, sp. n. http://zoobank.org/21D8B7CF-8BBE-4156-90B7-67F1C854AD8E Fig. 6

Holotype. Female, CNC, UNITED STATES. Holotype locality: Mount Evans, 3,658m, Clear Creek County, Colorado, USA.

Holotype labels. First label: Mt. Evans, COLO./12,000' 3 Aug./W.R.W.Mason '61. Second label: MIC CNC666529.

Paratype. 1 \bigcirc , 2 $\stackrel{?}{\circ}$ (CNC). Same locality than holotype, but collected at altitudes ranging from 4,023m (female) to 4,267m (males); collecting dates from 25.vii–4.viii.1961.

Diagnosis. This species can be separated from all other described species of *Microplitis* in North America by the combination of the following features: small size (body length 2.0–2.1 mm, fore wing length 1.7–1.8 mm), entirely dark brown to black coloration (including all legs), slightly infumated wings, very short antenna (its length not surpassing the length of mesosoma), apical flagellomeres cubic (about as long as wide), and high altitudinal distribution.

Description. Body dark brown to black (except for metatibia and al tarsi light brown). Wings slightly infumated, veins and pterostigma mostly brown. Head and mesosoma (dorsally) finely sculptured, metasoma mostly smooth dorsally, except for finely sculptured T1. Ovipositor sheaths smooth, almost without setae. Head not elongate; malar line shorter than mandible base; labrum, mandibles and glossa not enlarged; antennal flagellomeres 14–15 cubic (about as long as wide). Hypopygium not elongate





Figures 6. Microplitis altissimus, female holotype.

and not projecting beyond last tergum. Ovipositor sheaths relatively very small, barely visible beyond hypopygium. Fore wing with vein R1 much shorter than pterostigma. Legs with tarsal claws simple. Body measurements (mm). Body L: 2.1 (2.0); fore wing L: 1.8 (1.7); ovipositor sheaths L: 0.15 (approximate measurement); metafemur L/W: 0.59/0.15; metatibia L: 0.77; metatibia inner/outer spurs L: 0.13/0.12; first segment of metatarsus L: 0.33; F1/2/3/14/15/16: 0.14/0.11/0.10/0.07/0.07/0.11; ocular–ocellar line: 0.13; interocellar distance: 0.09; posterior ocellus diameter: 0.04.

Males. As females but with antenna of more normal length.

Distribution. United States: CO.

Etymology. From the Latin adjective 'altissimus', meaning 'the highest', referring to the locality at which all specimens were collected, currently the highest altitude of any known species of Microgastrinae in North America.

Comments. No biological or molecular data is known for this species. The small body and wings size, reduced antenna and short flagellomeres, and the dark coloration are all adaptions to living in a very cold, windy and harsh environment such as Mount Evans. The two male speciens were collected at 4,267m, by far the highest altitude recorded for any Microgastrinae in North America.

Microplitis jorgeluisi Fernandez-Triana, sp. n.

http://zoobank.org/AF9B3584-E65F-43AF-A93D-2B9162A2D0A7 Fig. 7

Holotype. Female, CNC, UNITED STATES. Holotype locality: Camp Maxey, Lamar County, Texas, USA.

Holotype labels. First label: USA: TX, Lamar Co./Camp Maxey/21.IX.-21.X.2003, MT/W. Godwin, SFASU/grassy site, lot # 88. Second label: MIC 000683.

Diagnosis. The combination of enlarged and acute hypopygium; long, thick, and smooth ovipositor sheaths; bilobate glossa; metafemur relatively very short and robust; and head laterally with antennal socket shelf-like are very distinctive and unique among all described species of Nearctic *Microplitis*. See above (under *M. julioalbertoi*) for further diagnostic characters to separate both species.

Description. Head and mesosoma black (except for orange-brown clypeus and labrum), metasoma mostly reddish-brown, legs mostly orange-yellow (except for brown coxae). Wings entirely infumated, veins dark brown, pterostigma brown with yellow spot at base. Head finely sculptured, mesosoma and metasoma mostly smooth dorsally (except for finely sculptured T1). Ovipositor sheaths smooth, almost without setae (only very few and short setae near apex). Head not elongate; malar line shorter than mandible base; labrum and mandibles not enlarged; glossa slightly elongate and bilobate. Hypopygium elongate and sharply acute, projecting considerably beyond last tergum. Ovipositor sheaths relatively long. Fore wing with vein R1 much shorter than pterostigma. Legs with tarsal claws simple. **Body measurements (mm).** Body L: 4.9; fore wing L: 4.4; ovipositor sheaths L: 0.85 (approximate measurement); metafemur L/W: 1.10/0.45; metatibia L: 1.54; metatibia inner/outer spurs L: 0.16/0.15; first segment of metatarsus L: 0.50; F1/2/3/14/15/16: 0.30/0.28/0.27/0.15/0.14/0.21; ocular–ocellar line: 0.24; interocellar distance: 0.22; posterior ocellus diameter: 0.10.

Distribution. United States: TX.



Figures 7. Microplitis jorgeluisi, female holotype.

Etymology. Named after my brother Jorge Luis, as appreciation for his love and for all the experiences we have lived together over the years (including helping me to collect insects).

Comments. No biological or molecular data is known for this species.

Microplitis juanmanueli Fernandez-Triana, sp. n. http://zoobank.org/1057486E-01AC-4E02-ABB9-D7D37AEC7D1D Figs 8

Holotype. Female, CNC, UNITED STATES. Holotype locality: Doolittle Ranch, Mount Evans, 2987m, Colorado, USA.

Holotype labels. First label: Doolittle Ranch/9800' Mt Evans,/COLO. 3-VIII/S. M. Clark '61. Second label: CNC497179.

Paratypes. $3 \ \bigcirc, 2 \ \oslash$ (CNC). USA, CO, Echo Lake, Mount Evans, 2,926–3,231m. **Other material examined.** $1 \ \bigcirc$ (CNC). Canada, BC, Atlin. Voucher codes: CNC281008, CNC281009, CNC281011, CNC281019, CNC841840, CNC841841.

Diagnosis. The extremely long metasoma of female (longer than the combined length of head and mesosoma) is unlike any other known *Microplitis*. That character, altogether with the very elongated hypopygium (which is almost twice as long as the last tergite, and considerably projects beyond it), the distinctive shape and sculpture of the ovipositor sheaths, and the elongated mouth parts, allow to unequivocally recognize the species.

Description. Body dark brown to black, legs mostly orange-yellow (except for coxae, anterior 0.1–0.2 of femora and metatarsus which are dark brown to black). Wings hyaline, with most veins dark brown but some veins on anterior half of wings (e.g., M+Cu and 1A) yellowish. Head and mesosoma extensively and coarsely sculptured, metasoma mostly smooth (except for strongly sculptured T1) and with very few setae on tergites. Hypopygium with relatively deep but sparse punctures. Ovipositor sheaths with strong sculpture (striae and punctures) on most of its surface. Head elongate, malar line longer than mandible base; labrum not enlarged; mandibles not enlarged nor strongly curved; glossa long; clypeus and face bulging centrally. Metasoma extremely elongate, longer than combined length of head and mesosoma, and representing approximately 0.6 of entire body length. Hypopygium very elongate, projecting considerably beyond last tergum. Ovipositor sheaths widened and rounded at apex. Fore wing with vein R1 slightly shorter than pterostigma. Legs with tarsal claws pectinate. Body measurements (mm). Body L: 5.7 (5.4–6.4); fore wing L: 4.2 (4.2–4.4); metasoma L: 3.6 (3.2-3.9); hypopygium L: 1.00 (0.98-1.06) ovipositor sheaths L: 0.45 (0.42-0.52); metafemur L/W: 1.01/0.30 (0.97-1.01/0.29-0.31); metatibia L: 1.38 (1.28-1.34); metatibia inner/outer spurs L: 0.20/0.20 (0.19-0.20/0.19-0.20); first segment of metatarsus L: 0.45 (0.42-0.43); F1/2/3/14/15/16: 0.23/0.26/0.24/0.13/0.11/0.17 (0.23-0.25/0.25-0.27/0.22-0.24/0.13/0.11-0.12/0.16-0.17); ocular-ocellar line: 0.19 (0.18); interocellar distance: 0.16 (0.16–0.17); posterior ocellus diameter: 0.09 (0.08 - 0.09).

Male. As in female, but metasoma of normal proportions.

Distribution. Canada, BC; United States, CO.

Etymology. This truly unique and exceptional species is named after my brother Juan Manuel, as appreciation for his love and for all the experiences we have lived together over



Figures 8. Microplitis juanmanueli, female holotype.

the years (including helping me to collect insects). Praying and hoping you can defeat the terrible cancer you are battling!

Comments. Because the long metasoma is only found in female specimens (also related to unique shape and sculpture of hypopygium and ovipositor sheaths), it can

be argued that those features are somehow related to parasitism; however until host caterpillars are found no further speculation is possible. This is one of the largest, most distinctive and unique species of Microgastrinae: at 6.4 mm of body length, one of the paratypes possibly represents the largest (although not the bulkiest) microgastrine wasp ever collected in North America -and indeed, even in the world very few species surpass that body length. However that size is only attained due to the disproportionately long metasoma (fore wing lengths, at 4.2-4.4 mm, are similar to that of large species of *Microplitis* and many other genera of Microgastrinae; as it is the rest of the wasp body). Beyond length, the species is also notable because of the shape and sculpture of hypopygium and ovipositor sheaths, head (with elongate mouth parts and clypeus and face bulging centrally), and shape and sculpture of T1-T2. In spite of so many unique morphological features, we still consider this species to belong to *Microplitis*, although whenever molecular data becomes available, the generic status might be revisited. The location of the female specimen from Atlin (Canada, BC) is thousands of kilometers apart from the localities of the Colorado specimens, but no morphological differences to separate them could be found. Until more is known, all are kept as one species (although the Canadian specimen is not considered as a paratype). No biological or molecular data is known for this species.

Microplitis julioalbertoi Fernandez-Triana, sp. n.

http://zoobank.org/51630C1F-BC61-4453-AF33-B2E7F15F56E6 Fig. 9

Holotype. Female, CNC, UNITED STATES. Holotype locality: Millen, Georgia, USA. Holotype labels. First label: Millen Ga./25.VIII.1957/J.G. Chillcott. Second label: CNC666523.

Paratype. 1 ^Q (CNC), United States: GA, Hiawassee, Towns County, 610m.

Other material. 1 \bigcirc (CNC), United States: CT, East Hartford.

Diagnosis. This is one of three species of *Microplitis* described in this paper with elongate mouth parts (the other two being *M. juanmanueli* and *M. mariamargaritae*). Until now, no *Microplitis* in North America had been reported to have that character. *M. julioalbertoi* has a much shorter and stout metafemur ($2.6 \times as$ long as wide; as compared with $2.8-3.3 \times in$ the other two species). It further differs from *M. mariamargaritae* in having an enlarged and acute hypopygium, with much longer ovipositor sheaths; and it can be separate from *M. juanmanueli* because of its normal-sized metasoma (metasoma being extraordinarily large in *M. juanmanueli*). *M. julioalbertoi* is also similar to *M. jorgeluisi*, but that species does not have elongated mouth parts, its palpi are yellow (dark brown in *M. julioalbertoi*) and the ovipositor sheaths do not have any setae (ovipositor with apical 0.3 with numerous setae which are as long as ovipositor sheaths width in *M. julioalbertoi*).

Description. Body reddish-brown, legs mostly orange-yellow (except for coxae). Wings entirely infumated, veins dark brown. Head finely sculptured, mesosoma and


Figures 9. *Microplitis julioalbertoi*, female holotype.

metasoma mostly smooth dorsally (except for strongly sculptured T1). Ovipositor sheaths smooth, with setae as long as sheaths width. Head elongate; malar line longer than mandible base; labrum large; mandibles very long and strongly curved; glossa

elongate. Hypopygium elongate and sharply acute, projecting considerably beyond last tergum. Ovipositor sheaths relatively long. Fore wing with vein R1 much shorter than pterostigma. Legs with tarsal claws simple. **Body measurements (mm).** Measurements (mm). Body L: 5.2 (5.2–5.5); fore wing L: 4.2 (4.3–4.5); ovipositor sheaths L: 0.95 (0.77–0.83); metafemur L/W: 1.04/0.40 (1.10/0.45); metatibia L: 1.54 (1.64); metatibia inner/outer spurs L: 0.16/0.16 (0.16/0.15); first segment of metatarsus L: 0.48 (0.49); F1/2/3/14/15/16: 0.27/0.26/0.25/0.14/0.13/0.20 (0.28/0.27/0.25/0.15 /0.15/0.19); ocular–ocellar line: 0.24 (0.22); interocellar distance: 0.22 (0.17); posterior ocellus diameter: 0.09 (0.09).

Distribution. United States: GA, CT.

Etymology. Named after my brother Julio Alberto, as appreciation for his love and for all the experiences we have lived together over the years (including helping me to collect insects).

Comments. The location of the female specimen from CT is roughly 1,500 kilometers north of the specimens from GA. However, no morphological differences to separate them could be found, and thus all are kept as one species for now (although the CT specimen is not considered as a paratype). No biological or molecular data is known for this species.

Microplitis mariamargaritae Fernandez-Triana, sp. n. http://zoobank.org/A6D67F7D-36A3-40B3-9249-546C82FCE646 Fig. 10

Holotype. Female, CNC, UNITED STATES. Holotype locality: Great Sand Dunes National Park and Preserve, 2316m, Colorado, USA.

Holotype labels. First label: COLO., Great Sand/Dunes Nat. Mon./1.VIII.68, 7600'/E.C.Becker. Second label: CNC666524.

Diagnosis. This is one of three species of *Microplitis* described in this paper with elongate mouth parts (the other two being *M. juanmanueli* and *M. julioalbertoi*). Until now, no *Microplitis* in North America had been reported to have that character. *M. juanmanueli* and *M. julioalbertoi* have enlarged and modified hypopygiums, whereas *M. mariamargaritae* has a normal sized hypopygium (i.e., not extending significantly beyond the tip of metasoma). Also *M. mariamargaritae* has a relatively narrow T1 (3.0 × as long as wide at posterior margin) which is parallel-sided for most of it length and then narrows toward posterior margin (thus anterior margin of tergite is wider than posterior margin); whereas in both *M. juanmanueli* and *M. julioalbertoi* T1 is relatively wider (at most 2.5 × as long as wide at posterior margin), with tergite widening towards posterior margin and only slightly narrowing on posterior 0.2 or less (but even then having anterior and posterior margins of tergite about the same width).

Description. Body dark brown to black, legs mostly orange-yellow (except for coxae). Wings infumated on anterior 0.6, with most veins dark brown. Head coarsely sculptured, mesosoma and metasoma mostly smooth dorsally. Ovipositor sheaths



Figures 10. Microplitis mariamargaritae, female holotype.

smooth. Head elongate; malar line longer than mandible base; labrum large; mandibles very long and strongly curved; glossa elongate. Fore wing with vein R1 much shorter than pterostigma. Legs with tarsal claws simple. **Body measurements (mm)**. Body L: 4.3; fore wing L: 4.2; ovipositor sheaths L: 0.40; metafemur L/W: 1.06/0.38;



Figure 11. Distribution map of the ten newly described species of Microgastrinae in North America.

metatibia L: 1.42; metatibia inner/outer spurs L: 0.15/0.15; first segment of metatarsus L: 0.55; F1/2/3/14/15/16: 0.30/0.28/0.27/0.17/0.15/0.20; ocular–ocellar line: 0.20; interocellar distance: 0.19; posterior ocellus diameter: 0.09.

Distribution. United States: CO.

Etymology. Named after my sister María Margarita, as appreciation for her love and for all the experiences we have lived together over the years (including helping me to collect insects).

Comments. No biological or molecular data is known for this species. Until now, seven endemic insect species had been recorded from the Great Sand Dunes National Park and Preserve (https://www.nps.gov/grsa/learn/nature/insects.htm). Thus *Microplitis mariamargaritae* becomes the eight endemic species from that significant natural area.

Acknowledgements

This research was supported by project AAFC-STB-1558 'Arthropod systematics research in support of Canadian Agriculture'.

References

- Dahlsten DL (1977) Parasitoids and predators of the Douglas-fir tussock moth, Orgyia Pseudotsugata (Lepidoptera: Lymantridae), in low to moderate populations in Central California. The Canadian Entomologist 109(5): 727–746. https://doi.org/10.4039/Ent109727-5
- Fernandez-Triana J (2010) Eight new species and an annotated checklist of Microgastrinae (Hymenoptera: Braconidae) from Canada and Alaska. Zookeys 63: 1–53. https://doi. org/10.3897/zookeys.63.565
- Fernandez-Triana J, Whitfield JB, Rodriguez JJ, Smith MA, Janzen DH, Hallwachs W, Hajibabaei M, Burns JM, Solis MA, Brown J, Cardinal S, Goulet H, Hebert PDN (2014) Review of *Apanteles* (Hymenoptera: Braconidae, Microgastrinae) from Area de Conservación Guanacaste, northwestern Costa Rica, with keys to all described species from Mesoamerica. ZooKeys 383: 1–565. https://doi.org/10.3897/zookeys.383.6418
- Fernandez-Triana J, Boudreault C (2016) Keylimepie peckorum gen. n. and sp. n., (Hymenoptera, Braconidae) from southern Florida, U.S., the first known brachypterous member of the subfamily Microgastrinae. ZooKeys 584: 95–107. https://doi.org/10.3897/zookeys.584.8319
- Karlsson D, Ronquist F (2012) Skeletal morphology of *Opius dissitus* and *Biosteres carbonarius* (Hymenoptera: Braconidae), with a discussion of terminology. PLoS ONE 7(4): e32573. https://doi.org/10.1371/journal.pone.0032573
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B 270: 313–321. https://doi.org/10.1098/ rspb.2002.2218
- Huber JT, Sharkey MJ (1993) Structure. In: Goulet H, Huber JT (Eds) Hymenoptera of the world: an identification guide to families. Agriculture Canada Research Branch, Monograph No. 1894E, Ottawa, Canada, 13–59.
- Ivanova NV, deWaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6: 998–1002. https://doi. org/10.1111/j.1471-8286.2006.01428.x
- Mason R (1987) Nonoutbreak species of forest Lepidoptera. Insect Outbreaks: 31–57. https:// doi.org/10.1016/B978-0-12-078148-5.50006-3
- Mason WRM (1981) The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): A phylogeny and reclassification of Microgastrinae. Memoirs of the Entomological Society of Canada, Ottawa, Canada, 147 pp.
- Muesebeck CFW (1921) A revision of the North American species of ichneumon-flies belonging to the genus *Apanteles*. Proceedings of the United States National Museum. 58: 483–576. https://doi.org/10.5479/si.00963801.2349.483
- Muesebeck CFW (1922) A revision of the North American ichneumon-flies, belonging to the subfamilies Neoneurinae and Microgasterinae. Proceedings of the United States National Museum. 61(2436): 1–76. https://doi.org/10.5479/si.00963801.61-2436.1
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes 7: 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

- Rivas LR (1964) A reinterpretation of the concepts "Sympatric" and "Allopatric" with proposal of the additional terms "Syntopic" and "Allotopic". Systematic Zoology 13(1): 42–43. https://doi.org/10.2307/2411436
- Rodriguez, JJ, Fernandez-Triana J, Smith MA, Janzen DH, Hallwachs W, Erwin TL, Whitfield JB (2013) Extrapolations from field studies and known faunas converge on dramatically increased estimates of global microgastrine parasitoid wasp species richness (Hymenoptera: Braconidae). Insect Conservation and Diversity 6: 530–536. https://doi.org/10.1111/icad.12003
- Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. http://www.simplemappr.net [accessed on 2017/12/08]
- Smith MA, Fernandez-Triana JL, Eveleigh E, Gómez J, Guclu C, Hallwachs W, Hebert PDN, Hrcek J, Huber JT, Janzen DH, Mason PG, Miller SE, Quicke DLJ, Rodriguez JJ, Rougerie R, Shaw MR, Varkonyi G, Ward D, Whitfield JB, Zaldívar-Riverón A (2013) DNA barcoding and the taxonomy of Microgastrinae wasps (Hymenoptera, Braconidae): impacts after 8 years and nearly 20 000 sequences. Molecular Ecology Resources 13: 168– 176. https://doi.org/10.1111/1755-0998.12038
- Snyder JR, Herndon A, Robertson WB (1990) South Florida rockland. In: Myers RL, Ewel JJ (Eds) Ecosystems of Florida. University of Central Florida Press, Orlando, 230–277.
- Valerio AA, Whitfield JB, Janzen DH (2009) Review of world *Parapanteles* Ashmead (Hymenoptera: Braconidae: Microgastrinae), with description of fourteen new Neotropical species and the first description of the final instar larvae. Zootaxa 2084: 1–49.
- Valerio AA, Whitfield JB (2015) Taxonomic review of the genus *Hypomicrogaster* Ashmead (Hymenoptera: Braconidae: Microgastrinae), with descriptions of 40 new species. Zootaxa 3979(1): 1–98. https://doi.org/10.11646/zootaxa.3979.1.1
- Whitfield JB (1985) The Nearctic species of *Deuterixys* Mason (Hymenoptera: Braconidae). Pan-Pacific Entomologist. 61(1): 60–67. https://doi.org/10.1139/z85-289
- Whitfield JB (1997) Subfamily Microgastrinae. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication No. 1, International Society of Hymenopterists, Washington, D.C., 333–364.
- Whitfield JB (2006) Revision of the Nearctic species of the genus *Pholetesor* Mason (Hymenoptera: Braconidae). Zootaxa 1144: 3–94.
- Williams DJM (1985) The New World genus *Lathrapanteles* n.gen.: Phylogeny and placement in the Microgastrinae (Hymenoptera: Braconidae: Cotesini). Canadian Journal of Zoology 63: 1962–1981.
- Williams DJM (1988) Classification, phylogeny and zoogeographic studies of species of Sathon Mason (Hymenoptera: Braconidae). Quaestiones Entomologicae 24: 529–638.
- Yu DSK, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015. Database on flash-drive. www.taxapad.com, Nepean, Ontario, Canada.

COMMENTARY



The Senticaudata, a suborder of the Amphipoda – A commentary on d'Udekem d'Acoz and Verheye (2017)

Alan A. Myers¹, Jim K. Lowry²

I School of Biological, Earth and Environmental Sciences, University College Cork, Cork Enterprise Centre, Distillery Fields, North Mall, Cork, Ireland 2 Australian Museum Research Institute, 6 College Street, Sydney, NSW 2010, Australia

Corresponding author: Alan A. Myers (bavayia@gmail.com); Jim K. Lowry (stephonyx@gmail.com)

Academic editor: C.O. Coleman | Received 9 November 2017 | Accepted 9 January 2018 | Published 18 January 2018

Citation: Myers AA, Lowry JK (2018) The Senticaudata, a suborder of the Amphipoda – A commentary on d'Udekem d'Acoz and Verheye (2017). ZooKeys 730: 151–155. https://doi.org/10.3897/zooKeys.730.22169

Abstract

A response is given to criticisms in a recent paper of the validity of the amphipod suborder Senticaudata. The tacitly assumed status of truth implied in some molecular higher phylogenies is called in to question.

Keywords

Amphipoda, classification, phylogeny, Senticaudata

Introduction

The suborder Senticaudata was established by Lowry and Myers (2013) based on a number of character states, but primarily on the important synapomorphy of apical robust setae on the rami of uropods 1 and 2. This character occurs in nearly 100 families and more than 5,000 species which form the suborder. The Senticaudata is recognised by the WoRMS online database and is cited by most taxonomic papers reporting on taxa in the group. The paper has been cited in at least 115 publications (Google Scholar). It has recently been included in a new phylogenetic classification of the Amphipoda (Lowry and Myers 2017).

Discussion

In a recent paper by d'Udekem d'Acoz and Verheye (2017), the validity of the amphipod suborder Senticaudata (Lowry and Myers 2013) is called into question. The argument put forward for questioning the status of the suborder, is that the main defining character state for this suborder proposed by Lowry and Myers (2013), the presence of apical robust setae on uropods 1 and 2, is also found to be present in a few taxa outside the Senticaudata. They comment:

Indeed, senticaudate taxa do not form a clade, suggesting that the distal ornamentation of uropods would be subject to homoplasy.

We absolutely agree that the said character state is homoplastic in some taxa and indeed we acknowledged this in our 2013 paper. However, the existence of homoplasies does not falsify a synapomorphy. The Senticaudata were not defined (as asserted by Verheye et al. (2016) by just "one alleged synapomorphy". The study by Lowry and Myers (2017) was based on 115 characters in the cladistic analysis, although the presence of apical robust setae on uropods 1 and 2 was one of the most important. Senticaudates also lack complex callynophores and brush setae. The Senticaudata includes nearly 100 families and more than 5,000 species that universally display this character state. The Senticaudata erected by Lowry and Myers (2013) was not a revolutionary concept, the great majority of taxa included therein had traditionally been recognised as an interrelated group. It had simply not been given taxonomic ranking before. Only very few taxa, outside the Senticaudata, have apical robust setae on uropods 1 and 2. Lowry and Myers (2013) described the situation in the Haustoriidae, where the convergence was attributed to their burrowing life style. In the case of the Idunellinae, mentioned by d'Udekem d'Acoz and Verheye (2017), the environmental factors over evolutionary time, leading to the convergence in this subfamily, cannot be determined. However, in the other subfamily of the Liljeborgiidae, the Liljeborgiinae, there are no robust setae on the apices of uropods 1 and 2. There are two possible scenarios to explain this situation. Either the Liljeborgiidae are senticaudates and the apical robust setae on uropods 1 and 2 have been lost in the subfamily Liljeborgiinae, or alternatively the Liljeborgiidae is not a senticaudate family and apical robust setae on uropods 1 and 2 have been convergently acquired by the subfamily Idunellinae. Like liljeborgiines, Idunellines have quite lanceolate uropods 1 and 2 even though they possess small apical robust setae. In addition, when we examined the other 114 characters that were employed in our cladistic study we found that the Liljeborgiidae aligned with the suborder Amphilochoidea. We therefore found it more parsimonious to place the Liljeborgiidae in the Amphilochoidea and assume that robust setae on the apices of uropods 1 and 2 were a homoplasy in the Idunellinae.

Some of the most difficult taxa to allocate in our study (Lowry and Myers 2013) were the Eusiridae and Calliopiidae. As we stated in our paper (Lowry and Myers 2013):

In this study, many of the clades are supported by several strong synapomorphies, but some inevitably are more weakly supported. Our aim in this work was to provide a complete classification, so we did not have the option of ignoring weakly supported clades.

Our classification was a hypothesis and like all scientific hypotheses it is open to falsification. We do not, however, accept that the Senticaudata is falsified by the simple discovery of a few taxa outside that suborder with robust setae on the apices of uropods 1 and 2. We agree with d'Udekem d'Acoz and Verheye (2017) that the presence of robust setae on the apices of uropods 1 and 2 is homoplastic. However, their argument, that the approximately 100 families of senticaudates with robust setae on the apices of uropod 1 and 2 compose so many homoplasies for this character state, that the taxa displaying it cannot be considered monophyletic, is rejected by us. We hypothesise that the senticaudates have inherited this character state as a homoplasy. Careful SEM studies of the apical setae of senticaudates and putative homoplastic taxa might prove informative. The Senticaudata are supported not by just one defining character state, but by our full cladistic analysis.

d'Udekem d'Acoz and Verheye (2017), claim that their earlier molecular phylogenetic analyses (Verheye et al. 2016), which focused on putative eusiroids but also included a representative sample of other amphipods did not support the validity of the suborder Senticaudata. In that study they selected 73 putative species of Eusiroidea for analysis, but they did not define on what basis these species were predetermined as eusiroid. The selection *a priori* of a eusiroid group may have affected their results. We, by contrast, did not select the Senticaudata *a priori*, it was our cladistic analysis that enabled us to recognize the clade Senticaudata. As stated in our paper (Lowry and Myers 2013): "approximately 300 characters were assembled in a DELTA database for the 212 families of world amphipods". In that paper we presented our findings for the Senticaudata, using a subset of 41 characters. Later (Lowry and Myers 2017), we published the full analysis with a subset of 115 characters. In our full analysis we selected the Amphipoda as our ingroup. This selection was *a priori*, but we felt that it was justified by the currently universal acceptance of the Amphipoda as a monophyletic group.

In their rDNA Bayesian tree of putative Eusiroidea (Verheye et al. 2016, fig. 3) they show taxa with the senticaudate character state in the same clade as taxa without the senticaudate character state. However, contrary to their assertion that robust setae on the apices of uropods 1 and 2 show multiple homoplasies, to the extent that the character state would "appear to disappear convergently" (Verheye et al. 2016) there are actually only three families with apical robust setae on uropods 1 and 2 among the nine clades of their putative Eusiroidea. One family is represented by a single genus, *Acanthonotozoma*. The robust setae on the apices of *Acanthonotozoma* are not homologous with the senticaudate character state. As pointed out by Just (1978) in his monograph on *Acanthonotozoma*, the apices of uropods 1 and 2 have "complexly inserted spines". They are more akin to embedded setae then they are to senticaudate apical setae. In addition *Acanthonotozoma* has character states that clearly place it in the

Iphimedioidea. The second family is the Pleustidae (of which they list two examples). In this family, uropods 1 and 2 are tending towards lanceolate rather than ferrulate and uropod 3 is clearly lanceolate, a character state that does not occur in the Senticaudata. The third family, the Calliopiidae (of which they quote numerous examples) does indeed exhibit the senticaudate character state and we classified them as Senticaudata (Lowry and Myers 2013). In addition to robust setae on the apices of uropods 1 and 2 the calliopiids also have ferrulate uropods 1–2 and a distoventral robust seta on urosomite 1, both character states of senticaudates.

In such a complex and extensive analysis as ours (Lowry and Myers 2017), involving over 200 families with 1,600 genera, we would expect that some families will prove to be wrongly assigned, but this would not falsify the Senticaudata, which comprise nearly 100 families supported by many synapomorphies.

It is not clear why the "other" amphipods are considered by d'Udekem d'Acoz and Verheye (2017) to be "representative". Representative of what? These "other" amphipods were derived from what the authors define as non-eusiroid sequences selected from the study of Englisch (2001). In what way this selection of amphipod taxa, which appear to be unrelated to their study, can test the validity of the Senticaudata is not explained. We might also add, that the relationships shown by these non-eusiroid taxa are unprecedented. For example, in their maximum likelihood tree (Verheye et al. 2016, fig. 2), Atylus and Byblis (Dexaminidae and Ampeliscidae) are sister taxa to Bathyporeia, (Gammaroidea); Salentinella (Bogidiellidae) is a sister taxon to Haustorius (Haustoriidae); Stegocephalus (Stegocephalidae) is a sister taxon to Antatelson (Stenothoidae) and Syrrhoe (Synopiidae) is a sister to Bactrurus/Crangonyx (Crangonyctidae). During the three centuries that scientists have turned their attention to amphipod relationships, none of these associations have ever before been suggested. Whereas our concept of the Senticaudata is not in any way revolutionary, some of the relationships suggested by Verheye et al. (2016) in their analyses are radical. Yet there is no justification provided by these authors in support of these relationships. In the analyses by Verheye et al. (2016) gene sampling was low and the two genes used were not fully congruent with each other, so criticism of any existing classification is weakly based.

Molecular studies of higher phylogeny cannot be considered as the truth. Much has still to be learned about molecular evolution. Genes can also be homoplastic. It would be statistically improbable that any given base pair substitution, occurring by random mutation in a neutral gene, could have occurred only once in evolutionary history. It is likely that homoplasy is common in the genotype as well as in the phenotype, even where neutral genes are concerned. Molecular approaches have been shown to give meaningful results at population level and may perhaps reflect real relationships at species level. However, it appears that at higher taxonomic levels the effectiveness of current molecular methods decreases, so that higher phylogenetic relationships are not reliable. This can be seen in the study by Verheye et al. (2016), where the relationships shown in their "representative sample of other amphipods" are inexplicable.

References

- d'Udekem d'Acoz C, Verheye ML (2017) *Epimeria* of the Southern Ocean with notes on their relatives (Crustacea, Amphipoda, Eusiroidea). European Journal of Taxonomy 359: 1–553. https://doi.org/10.5852/ejt.2017.359
- Englisch U (2001) Analyse der Phylogenie der Amphipoda (Crustacea, Malacostraca) mit Hilfe von Sequenzen des Gens der RNA der kleinen ribosomalen Untereinheit. PhD Thesis, Fakultat fur Biologie, Ruhr – Universitat Bochum, Bochum.
- Just J (1978) Taxonomy, Biology, and Evolution of the Circumarctic Genus *Acanthonotozoma* (Amphipoda), with Notes on *Panoploeopsis*. Acta Arctica 20: 1–140.
- Lowry JK, Myers AA (2013) A Phylogeny and Classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). Zootaxa 3610(1): 1–80. https://doi.org/10.11646/ zootaxa.3610.1.1
- Lowry JK, Myers AA (2017) A Phylogeny and Classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida). Zootaxa 4265(1): 1–89. http://dx.doi.org/10.11646/zootaxa.4265.1
- Verheye M, Martin P, Backeljau T, d'Udekem d'Acoz C (2016) DNA analyses reveal abundant homoplasy in taxonomically important morphological characters of Eusiroidea (Crustacea, Amphipoda). Zoologica Scripta 45(3): 300–321, supplements S1–S3. https://doi.org/10.1111/zsc.12153