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An insight into the tribe *Hexathrombiini* (Actinotrichida: Trombidioidea, Microtrombidiidae, Eutrombidiinae) with new data on host-parasite interaction

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Abstract
The status of the genera in the small microtrombidiid mite tribe Hexathrombiini is reevaluated. Type specimens representing all genera were studied and diagnostic characters for Hexathrombiini are reviewed, summarized, and new data and a key to the genera in the tribe are provided: *Alhamitrombium*, *Beronium*, *Hexathrombium* and *Hoplothrombium*. *Hexathrombium* is the most speciose genus in the tribe and species recorded from South America are compared, as well as those with a divided pygidial plate. A provisional key to species assigned to *Hexathrombium* is provided. Finally, *Hexathrombium abirami* was captured in Peru parasitizing a bright metallic tiger beetle (*Tetracha fulgida*). A total of 361 larvae were removed parasitizing a single carabid host; this is the highest load of parasites reported in terrestrial Parasitengona mites associated with arthropods. This capture represents a new record of Hexathrombiini mites for Peru. A redescription of *He. abirami* using all specimens available to date is included.

Keywords: *Parasitengona,* Alhamitrombium*,* Beronium*,* Hexathrombium*, morphology*

Introduction

The tribe Hexathrombiini Fain & Drugmand, 1993 (see Discussion section for authorship) was erected within Eutrombidiinae Thor, 1935 to accommodate *Hexathrombium* Cooreman, 1944, *Beronium* Southcott, 1986 and *Hoplothrombium* Ewing, 1925. Later, Mayoral & Barranco (2005a) described *Alhamitrombium* in Hexathrombiini. Fifteen species, variously distributed within the six zoogeographic regions, have been described in the tribe to date. All remain known exclusively from larvae that parasitize carabids (including formerly distinguished Cincindelidae) and staphylinid beetles. There are two exceptions: *Hoplothrombium quinquescutatum* Ewing, 1925 reported on a single specimen adhering to an Oribatida mite taken from the stomach of a toad (Ewing 1925), and *Hexathrombium southcotti* Zheng, 1997 captured from ichneumonid wasps (Zheng 1997; Felska et al. 2018). Haitlinger (1999) considered the latter to be probably an accidental host. Most species are known only from few specimens, and they have been recorded from single localities; as an exception, more than 40 specimens of *Beronium laemostenis* Mayoral & Barranco, 2005 have been collected from 10 different localities (caves) in Spain (Mayoral & Barranco 2005b; Mayoral 2013).

The most speciose genus is *Hexathrombium* and it contains the species: *Hexathrombium cicindelae* (Floch & Abonnenc, 1941), *Hexathrombium abirami* Haitlinger, 1997, and *Hexathrombium marittae* Haitlinger, 1994 – from the Neotropical region; *Hexathrombium lubomirae* (Haitlinger, 1994) – from the Afrotropical and Oriental Region; *Hexathrombium fageli* Fain & Drugmand, 1993 and *Hexathrombium spatuliferum* Cooreman, 1944 – from the Afrotropical region; *Hexathrombium willisi* Southcott, 1993 – with Nearctic distribution; *Hexathrombium sorayae* Haitlinger, 1994 and *He. southcotti* – with Palaearctic

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distribution; and *Hexathrombium mamerti* Haitlinger, 1999 – from the Australian region. Two other findings from South America refer to uncertain identifications of specimens assigned to *He. cf. marittae* and *He. cf. cicindelae* (Pérez-Espinoza & Moreno Salas 2016; Almada & Cédola 2017).

The genus *Beronium* Southcott, 1986 was erected by Southcott (1986) to accommodate *Hoplothrombium coiffaiti* Beron, 1973. This genus is known from the south-western Palaearctic, and comprises *Beronium coiffaiti* (Beron, 1973), *Beronium veronicae* Haitlinger, 1994 and *B. laemostenis* (Beron 1973; Haitlinger 1994; Mayoral & Barranco 2005b; Mayoral 2013). The monotypic genera *Hoplothrombium* Ewing, 1925, and *Alhamitrombium* Mayoral & Barranco, 2005 are known from the Nearctic and Palaearctic regions, respectively (Ewing 1925; Vercammen-Grandjean 1967; Mayoral & Barranco 2005a); they include the species *Ho. quinquescutatum* and *Alhamitrombium tetraseta* Mayoral & Barranco, 2005.

Welbourn (1983) listed *Ho. quinquescutatum* and *Ho. coiffaiti* under *Hoplothrombium*, in addition to the species *Trombidium cicindelae* Floch & Abonnenc, 1941 and *He. spatuliferum*. The generic affiliation of "*coiffaiti*", "*cicindelae*" and "*spatuliferum*" was not followed by subsequent authors since those specimens do not comply with the generic diagnosis of the genus and *Hoplothrombium* has therefore remained monotypic.

Here, we redescribe *Hexathrombium abirami* from new specimens collected in Peru, parasitizing *Tetracha fulgida* (Klug, 1834) (Carabidae). The load of parasites reported here for *T. fulgida* is the highest infestation record of terrestrial Parasitengona mites associated with arthropods. The diagnostic traits for the four genera in Hexathrombiini were reviewed and representatives of the different genera were studied (except *Hoplothrombium* that we relied on published descriptions). An updated list of relevant characters, a key to the genera in Hexathrombiini and a provisional key to *Hexathrombium* species are provided.

Material and methods

A specimen of *T. fulgida* infested by larvae was collected in Peru (dept. Huánuco, Rio Yuyapichis, ACP Panguana, 9°37′S, 74°56′W, 230 m.a.s.l.), 01.-05–21.05.2015, by S. Friedrich, F. Wachtel and M. Steinherr. The material was preserved in 80% Ethanol.

Larvae were detached from the host with an entomological pin and mounted on microscopic slides in Hoyer's medium. The overall number of larvae attached to the host was counted and the measurements were taken using NIS-Elements Br software, under a Nikon Eclipse E600 microscope coupled with DS-Fi1 camera system. Photos were taken with a DS-Fi3 camera attached to a Nikon Eclipse 80i microscope and the images were stacked using Helicon Focus software (© Helicon Soft Ltd., 2000). All measurements are given in micrometers. The terminology follows Southcott (1993), Vercammen-Grandjean (1967) and Wohltmann et al. (2007). The material (slide-mounted and alcohol preserved larvae; host specimen) is deposited in the Department of Invertebrate Systematics and Ecology, Wrocław University of Environmental and Life Sciences, Poland (DISE WUELS). Five larvae (slide-mounted) are deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM).

For the purpose of comparison and re-appraisal of characters used in the diagnosis of Hexathrombiini, the type material of *He. abirami*, *He. lubomirae*, *He. marittae*, *He. mamerti*, *B. veronicae*, *B. laemostenis* and *A. tetraseta* was studied. The references to other members of the tribe are based on original descriptions.

Results

Hexathrombiini Fain & Drugmand, 1993

Hexathrombiini Fain & Drugmand, 1993: 123.
Hexathrombiini: Southcott 1993: 943.

Diagnosis (after Fain & Drugmand 1993; Southcott 1993, verified).

Larva. Idiosoma constricted behind the level of coxae III, covered with scutum and four median shields, encompassing the bases of setae c_1, d_1, e_1 and h_1; the posterior-most shield may be divided into two separate sclerites. Eyes sessile, each composed of two lenses (*Hexathrombium*), one lens (*Hoplothrombium* and *Alhamithrombium*) or eyes reduced to ocular plates (*Beronium*). Scutum bearing non-sensillary setae (AM, AL, PL) and a pair of sensilla (S). fCx = 2-1-1 or 2-2-2. Medial coxala I (*1a*) simple. Setae on coxae II and III modified (short, thickened) or simple. Tarsi I and II terminated with two claws and empodium. Tarsus III highly modified, terminated with two claws and lophotrix ("penicala" *sensu* Southcott 1993). Inner (posterior) claw short and robust, median claw long, falciform. Lophotrix shifted to dorsodistal part of the segment. Gnathosoma with stephanostome. Hypostomalae thick, short.

Active postlarval forms. Not known.

Type genus. Hexathrombium Cooreman, 1944

Genera included. Hexathrombium Cooreman, 1944; *Hoplothrombium* Ewing, 1925; *Beronium* Southcott, 1986; *Alhamitrombium* Mayoral & Barranco, 2005.

Remarks. The position of seta *1a* may indistinctly vary in all genera in question, as the seta is inserted close to the coxal plate margin and its actual location in the mounted specimens may be considered dubious. Vercammen-Grandjean (1967) considered *1a*, observed within the coxal plate in *Ho. quinquescutatum*, a "migrated sternal seta".

The chaetotaxy of terminal leg segments (Ge – Ta I, Ge – Ta II, Ge – Ta III), with special reference to specialized setae, has been variously interpreted due to the difficulties in their visualization, specially their actual nature and presence. The more detailed close-up to the setae, should be carried out to clarify their actual state in all members of the genus.

The highly modified termination of tarsus III is similar in all Hexathrombiini and differs to those observed in Eutrombidiini. Southcott (1993) described in Hexathrombiini the presence of a branched seta ("penicala" *sensu* Southcott 1993) on the dorsodistal projection of tarsus III, and also two claws located ventrodistally. From those, the median claw is long, falciform and simple, whereas the posterior claw (i.e. smilum) (anterior claw *sensu* Southcott 1993) is in the form of a short and thick hook with a dorsal spur-like process. In Eutrombidiini, there is a moustache-shaped seta about 3/4 along the dorsum of tarsus III ("cultala" *sensu* Southcott 1993), a multipronged seta with several large setules arising dorsally at the distal end of tarsus ("dumala" *sensu* Southcott 1993), and a thickened setae with setules in the ventrodistal portion of the tarsus ("calcanala" *sensu* Southcott 1993) (Southcott 1993). Husband and Wohltmann (2011) observed in *Eutrombidium* the presence of a scopa on tarsus III ("cultala" *sensu* Southcott, 1993) and lophotrix ("dumala" *sensu* Southcott 1993). Despite the different position of branched, pectinate seta in Hexathrombiini (seta shifted to a dorsodistal position), its structure is congruent with the lophotrix observed in Eutrombidiini and also in some other microtrombidiid mites. The short and thick inner claw located ventrodistal and covered with few bristles should be considered a smilum. Another modified seta, a scopa, is absent in Hexathrombiini.

Hexathrombium **Cooreman, 1944**

Hexathrombium Cooreman, 1944: 1.
Hexathrombium: Southcott 1993: 945.

Diagnosis (after Southcott, 1993, verified).

Larva. The posterior-most shield on dorsal idiosoma (pygidial shield, Q5) entire (*He. marittae, He. lubomirae, He. willisi*) or divided into two separate sclerites (*He. abirami, He. cicindelae, He. fageli, He. mamerti, He. sorayae, He. southcotti, He. spatuliferum*). Eyes composed of two lenses inserted in ocular plates. Odontus bifid. fCx = 2-1-1. Medial coxala I (*1a*) simple (spike-like or slender, tapering). Lateral coxala I (*1b*), coxalae II (*2b*) and III (*3b*) bilobed, with diverged processes (in *He. willisi – 1b, 2b, 3b* - bilobed, with indistinctly diverged, rounded apically processes). Seta *3a* shifted to intercoxal position or absent. Pre-anal tubercle present. fV = 12–16 (18–20 in *He. southcotti*); for comparison of character state in South American species see Table III. Hypostomala reniform.

Type species. Hexathrombium spatuliferum Cooreman, 1944

Species included and country records. He. abirami, Brazil, Peru; *He. cicindelae*, French Guiana; *He. fageli*, Ethiopia, Ivory Coast; *He. lubomirae*, Madagascar, Sumatra; *He. mamerti*, Australia; *He. marittae*, Chile; *He. sorayae*, China; *He. southcotti*, China; *He. spatuliferum*, Zaire; *He. willisi*, USA. Additional records: *He. cf. cicindelae*: Almada & Cédola (2017), Argentina; *He. cf. marittae*: Pérez-Espinoza & Moreno Salas (2016), Chile. Welbourn (1983) reported two presumably new species of *Hoplothrombium* from Ecuador; they were never formally described, however, they both should be placed in *Hexathrombium* (Cal Welbourn, pers. comm.).

Hosts. Coleoptera: Carabidae, Erotylidae, Staphylinidae; Hymenoptera: Ichneumonidae (see also Table IV).

Redescription of *Hexathrombium abirami* Haitlinger, 1997

Hexathrombium abirami Haitlinger, 1997: 81.

Diagnosis Larva. Pygidial shield (Q5) divided. Coxalae *1a* shifted to the margin of coxal plates, slender, tapering. Coxalae *1b* and *2b* bilobed, with horizontally diverged processes.

Description. Metric data provided in Table I (except for few dimensions given below).

Gnathosoma (Figure 1(a,b)) compact, with well-sclerotized frames of subcapitulum, chelicerae and palps. Stephanostome present. Internal horseshoe-like sclerite inserted between inner and outer cuticular sheath. One pair of nude adoral setae (*or*). Subcapitular setae reniform. Cheliceral claws distinctly curved. Palps relatively small and robust. fP_p = 0-N-N-NNB2-BNNNNNωζ. Seta on palp femur and palp genu short, thorn-like. Two setae on palp tibia short, thorn-like, the third seta long, with 1–2 fine barbs. Odontus bifid. The longest, most proximal seta on palp tarsus with few (2–3) indistinct barbs only. Palpal supracoxalae (*elcp*) not detectable.

Supplementary measurements, not included in the Table I (format: mean (range)), for 10 specimens from Peru: GL = 101 (90–111), PaFe = 13 (11–15), PaGe = 9 (7–10), PaTi = 9 (8–11), PaTa = 7 (6–8), Odo = 6 (5–7), Ch base = 87 (77–104), Ch claw = 18 (13–24), *bs* = 10 (8–12).

Dorsal idiosoma (Figure 2) oval, slightly constricted behind the level of coxae III, rounded at anterior and posterior termination. Integument, except for sclerites, folded in lines. Scutum (Q1) (Figures 2 and 3) pentagonal in outline, rounded anteriorly, bearing paired, non-sensillary setae AM, AL, PL, and a pair of sensilla (S). Antero-lateral parts of scutum with linear pattern, medial part of the sclerite porous. Posterior margin almost straight, bordered with delicate lamellar band. Additionally, small octal-shaped or semi-oval mark, probably representing the less sclerotized part of the sclerite, present antero-laterally in lower layer of scutum (or [?] immediately under the scutum surface), on each side of symmetry axis. Bases of sensilla located between AL and PL bases, closer to PL and slightly shifted to medial position. AM smooth or with 1–2 barbs, AL, PL and S with few barbs along entire stem length. Paired eye lenses (Figure 2), each pair on a common, weakly sclerotized plate located close to the postero-lateral margins of the prodorsal sclerite (Q1). Scutellum (Q2) trapezoidal in shape, with a pair of c_1 setae. Second and third scutellum (Q3, Q4) with a pair of d_1 and e_1 setae, respectively (in one specimen (7802/13) with duplicated seta e_1 on Q4 sclerite); both sclerites rectangular in shape, with rounded corners. Setae e_1 located close to the anterior margin of Q4. The fifth shield (Q5) divided into two separated, oval plates, each bearing a h_1 seta. fD: (2) 4-(2)4-(2)4-6-(1 + 1)2 = 28. Setae in rows C, D, E, F, except for c_1, d_1, e_1, located on small platelets; stems of setae in C-F rows only slightly narrowed at termination and covered with short barbs along the entire length. Setae c_3, d_3, e_3 slightly shorter than other setae in the respective rows C-E. Setae h_1 and h_2 longer than the preceding setae, distinctly narrowed apically; h_2 inserted in roundish plates (of diameter similar to the width of h_1 plates, i.e. Q5/2); shafts of h_2 slenderer than those of h_1 and with distinct setules.

Ventral idiosoma (Figure 4). Coxal plates (I – triangular in outline, II – rectangular, rounded at base, III – square-shaped in outline) well sclerotized along the anterior border; the posterior border weakly marked or discontinuous. Anterolateral part of coxa I frame as well as its distal portion strongly sclerotized (Figure 4); sclerotization of the respective parts of coxae II and III less pronounced. Claparède's organs (*clp*) present at posterolateral corner of coxa I. Coxa I with two setae, medial coxala (*1a*) normal, nude, tapering, placed on cuticular band forming the medial extension of the most sclerotized part of coxal frame; lateral coxala (*1b*) modified, bilobed (Figure 6(a)); coxa II and coxa III with one modified, bilobed seta each (*2b* and *3b*, respectively); all modified coxalae (*1b*, *2b*, *3b*) with horizontally diverged processes (lobes); lobes indistinctly narrowing at termination and slightly extending beyond the setal base (widely diverging in *2b*, making the seta the widest in comparison with *1b* and *3b*). Setae *3a* (20 long) simple, slender, nude, and located between coxae III. Supracoxalae of coxae I (*elc I*) not detectable. fV: 4-4u-4-2 = 14. Ventral setae tapering, with thinner shafts than dorsal setae. Anal opening surrounded with membraneous valves, anal sclerites absent. Pre-anal protuberance (tubercle) present, circle-like, similar in diameter to the length of anus, and located anterior to excretory slit. The tubercle, slightly elevated above the idiosoma surface, surrounded with more sclerotized, porous sides.

Legs (Figure 5(a–c)). Segmentation formula 6-6-6. For leg chaetotaxy see Table II. Normal setae on legs setulated to smooth. Robust, fan-like seta present in distal part of tarsus II. Tarsi I and II terminated with two claws and empodium. Claws similar in length, covered with onychotrichs. Empodium claw-like, slightly spatulate distally. Tarsus III highly modified at termination, with lophotrix in dorsodistal position and two claws located ventrodistal. Lophotrix composed of one branch, with one long, proximal, secondary branch on one side and with several, gradually shortening, secondary and tertiary branches on the other (Figure 7(a)). Inner claw short, robust, with small spurs; medial claw long, falciform.

Material examined. Holotype and two paratypes, deposited in the Museum of Natural History, University of Wroclaw, Poland. Ten larvae collected on *T. fulgida* from Peru in 2015 (present study) and randomly selected from a sample of 361 specimens parasitizing one host (for details – see Material and methods).

Table I. Metric data for *Hexathrombium* spp. Species with divided pygidial shield Q5: *He. abirami, He. cicindelae, He. fageli, He. mamerti, He. sorayae, He. southcotti, He. spatuliferum*. Species with undivided pygidial shield: *He. marittae, He. lubomirae*. For *He. willisi* see Southcott (1993).

species	*He. cicindelae* (Floch & Abonnenc, 1941)	*He. cf. cicindelae*	*He. spatuliferum* Cooreman, 1944	*He. fageli* Fain & Drugmand, 1993	*He. marittae* (Haitlinger, 1994)	*He. cf. marittae*	*He. sorayae* (Haitlinger, 1994)	*He. abirami* Haitlinger, 1997	*He. abirami* Haitlinger, 1997	*He. southcotti* Zheng, 1997	*He. mamerti* Haitlinger, 1999	*He. lubomirae* (Haitlinger, 1994)
Source of data	Floch & Abonnenc (1941)	Almada & Cédola (2017)	Fain & Drugmand (1993)	Fain & Drugmand (1993)	Present study (type material)	Pérez-Espinoza & Moreno Salas (2016)	Haitlinger (1994)	Present study (type material)	Present study (new data)	Zheng (1997)	Haitlinger (1999)	Haitlinger (1994)
Distribution	[South America]	[South America]	[Afrotropic]	[Afrotropic]	[South America]	[South America]	[Palaearctic]	[South America]	[South America]	[Palaearctic]	[Australia]	[Sumatra, Magadascar]
Sample size/ data layout	Sample size not known	Mean (range)[2] sample size not known	(range) n = 2	(range) n = 3	Mean (range) n = 7[1]	Mean (range)[2] n = 25	(range) n = 3	Mean (range) n = 3[1]	Mean (range) n = 10	n = 1	(range) n = 9	n = 7[7]
IL	630–760[4]	492 (545–610)[3]	590–630	447–468	473 (417–563)	–	336–576[3]	632 (581–667)	673 (564–761)	470	463–527[3]	404–704[3]
IW	280–430	287 (305–370)	300–302	195–222	236 (203–284)	–	192–328	353 (292–389)	388 (286–465)	250	216–266	208–408
IL/IW	–	–	2.0–2.1	–	2 (1.7–2.2)	–	1.7–2.0	1.8 (1.7–2.0)	1.7 (1.6–2.0)	1.9	–	–
Scutum L	–	[?]146 (132–150)	165–180	140–146	172 (166–178)	–	184–208	192 (187–195)	164 (145–175)	160	148–164	180–198
Scutum W	–	–	166–177	120–135	160 (158–165)	–	166–190	184 (182–187)	154 (138–168)	170	136–148	164–184
AM	–	–	–	30–39	32 (27–37)	–	30–34	32 (31–33)	35 (25–42)	27	28–36	34–44
AA	–	–	74–75	45–47	77 (75–80)	–	80–82	94 (91–98)	73 (67–82)	74	64–72	74–84
MA	–	87 (82–98)	85–99	66–74	74 (73–75)	72 (64–84)	96–104	106 (104–107)	93 (81–105)	98	76–84	98–114
AL	–	–	51–56 (broken)	30–45	44 (42–46)	–	28–32	54	43 (37–48)	30	40–46	32–38
AW	–	108 (102–113)	128–138	43–90	128 (125–132)	–	134–142	148 (145–153)	119 (104–132)	128	106–114	138–150
PL	–	25 (22–30)	32–36	25–38	24	–	18–20	31 (30–32)	30 (27–32)	20	24–30	14–16
PW	–	139 (130–147)	153–165	120–133	148	152 (142–167)	164–180	178 (169–186)	146 (133–162)	155	124–132	160–180
AP	–	34 (30–37)	42–45	39–45	58 (55–61)	59 (54–75)	28–32	49 (44–54)	39 (35–42)	32	38–44	28–32
S	–	–	76–85	65–75	84 (79–89)	–	–	–	106 (93–123)	116	82–96	100–116
SB	–	101 (92–107)[4] 91 (75–108)[4]	115–120	93–99	117 (110–121)	121 (116–136)	128–140	137 (132–140)	112 (94–126)	118	90–104	128–144
ASB	–	–	140–150	120–122	141 (130–148)	–	154–184	165 (164–166)	138 (120–151)	128	122–140	160–190
PSB	–	–	29–30	20–25	31 (26–36)	–	24–30	27 (21–31)	26 (22–32)	10	20–26	20–24
PSL (HS)	–	–	60–66	57–60	60 (55–70)	–	68–82	60 (56–63)	56 (49–65)	62	50–62	72–82

(*Continued*)

Table I. (Continued).

species	*He. cicindelae* (Floch & Abonnenc, 1941)	*He. cf. cicindelae*	*He. spatuliferum* Cooreman, 1944	*He. fageli* Fain & Drugmand, 1993	*He. marittae* (Haitlinger, 1994)	*He. cf. marittae*	*He. sorayae* (Haitlinger, 1994)	*He. abirami* Haitlinger, 1997	*He. abirami* Haitlinger, 1997	*He. southcotti* Zheng, 1997	*He. mamerti* Haitlinger, 1999	*He. lubomirae* (Haitlinger, 1994)
PSW (LSS)	–	–	150–171	128–130	169 (162–180)	–	170–192	177 (171–184)	145 (128–168)	120	124–154	172–202
PLN	–	29 (28–30)	18–30	36–39	23 (23–24)	–	–	29 (28–30)	31 (26–38)	25	–	19[7]
QL (SL)	–	35 (35–40)[5] 35 (30–40)[5]	50–51	36–39	41 (39–44)	42 (39–49)	[?] 50	–	41 (38–44)	70	44–46	54–60
QW (SS)	–	50 (41–57)	57	42–52	64 (56–69)	32 (28–39)	76–78	72 (71–73)	60 (50–69)	65	46–64	80–100
L3	–	–	33–39	23–26	34 (28–41)	–	30	39 (39–40)	34 (28–38)	30	30–38	36–40
W3	–	–	103–118	75–86	107 (101–119)	–	106–120	118 (111–125)	95 (81–118)	110	72–86	112–126
PLN3	–	18 (18–20)	13–21	12–15	13 (12–14)	–	–	20 (19–20)	19 (15–22)	20	–	18[7]
QL3	–	38 (35–43)	51–58	40–45	43 (39–48)	–	60	58	45 (36–51)	70	[?]52	68–74
QW3	–	–	45–50	30–48	47 (42–51)	–	44–60	57 (54–61)	43 (35–56)	50	36–44	54–68
L4	–	–	36–41	30–32	40 (32–46)	–	34–36	39 (36–43)	41 (35–49)	35	36	36–44
W4	–	–	96–108	57–64	107 (100–111)	–	100–104	113 (100–126)	98 (82–111)	[?]30[8]	[?]64–74	106–120
PLN4	–	21 (20–23)	15–19	16–18	13	–	–	18 (17–18)	20 (16–25)	22	–	25[7]
QL4	–	41 (38–45)	51–56	42–48	51 (50–54)	–	[?]52–72	54	46 (41–52)	70	[?]54–56	80–90
QW4	–	–	47–48	24–35	61 (56–70)	–	66–72	57 (54–62)	54 (42–69)	30	36–52	78–94
L5	–	34 (33–38)	36	21–24	47 (44–50)	–	38–42	42 (39–44)	41 (36–47)	–	30–36	28–36
W5	–	–	21–24	15–18	57 (47–68)	–	54–60[5]	28 (24–32)	23 (15–30)	40	–	44–52
PLN5	–	22 (20–25)	–	–	18 (17–20	–	–	23	23 (20–26)	–	–	16[7]
QL5	–	67 (52–75)	70–75	45	53 (49–57)	54 (44–64)	82–90	84 (78–91)	68 (60–75)	90	70–78	102–114
QW5	–	31 (28–35)	35–36	25–28	26 (23–30)	–	24–26	36 (34–39)	42 (30–52)	25	24–28	22–26
DS	–	–	34–60	30–48	29–53	–	30–64	(33–67)	(28–60)	50–70	36–52	20–74
A lens	–	–	–	–	13	–	–	14 (13–15)	11 (8–12)	–	–	–
P lens	–	–	–	–	9	–	–	13 (12–14)	8 (6–10)	–	–	–
Ocular sclerite [L]	–	–	–	–	40	–	28–30	–	32 (29–37)	–	28–34	30–32
Cx I	–	62 (50–68)	–	–	49	–	68–76	69 (64–72)	68 (62–75)	–	58–72	70–80
Tr I	–	–	–	–	30 (25–33)	–	34–42	38 (34–41)	32 (29–39)	–	32–36	36–40
Fe I	–	47 (45–50)	50–54	47–51	49 (48–51)	–	48–54	59 (56–60)	54 (49–60)	–	42–50	50–60
Ge I	–	18 (18–20)	22–26	18–22	20 (18–22)	–	18–20	21 (21–22)	19 (17–22)	–	18–22	22–24
Ti I	–	31 (28–35)	36–39	31–35	29 (26–33)	–	32–36	40 (39–41)	36 (31–41)	–	32–36	34–40
Ta I	–	52 (50–53)	67–69	60–68	70 (64–77)	–	64–66	72 (69–73)	65 (60–69)	–	50–56	60–70
Leg I	–	–	–	–	254	–	266–288	298 (294–302)	275 (257–303)	290[6]	244–268	–
Cx II	–	58 (55–60)	–	–	51 (50–52)	–	52–60	60 (57–62)	60 (53–70)	–	44–54	52–56
Tr II	–	–	–	–	31 (30–32)	–	34–42	38 (34–43)	30 (26–35)	–	28–32	34–44
Fe II	–	35	45–48	45	39 (38–40)	–	30–38	47 (44–49)	44 (39–47)	–	32–42	44–52
Ge II	–	16 (15–18)	17–18	15–16	14 (11–16)	–	14–18	15 (14–16)	15 (12–17)	–	16–18	16–20

(*Continued*)

Table I. (Continued).

species	*He. cicindelae* (Floch & Abonnenc, 1941)	*He. cf. cicindelae*	*He. spatuliferum* Cooreman, 1944	*He. fageli* Fain & Drugmand, 1993	*He. marittae* (Haitlinger, 1994)	*He. cf. marittae*	*He. sorayae* (Haitlinger, 1994)	*He. abirami* Haitlinger, 1997	*He. abirami* Haitlinger, 1997	*He. southcotti* Zheng, 1997	*He. mamerti* Haitlinger, 1999	*He. lubomirae* (Haitlinger, 1994)
Ti II	–	27 (25–30)	30–34	24–27	23 (20–25)	–	26–32	29 (26–31)	27 (22–30)	–	20–30	28–32
Ta II	–	43 (43–45)	49–51	42–48	49 (44–53)	–	44–48	53 (51–54)	49 (45–52)	–	40–50	48–56
Leg II	–	–	–	–	–	–	200–234	241 (238–243)	224 (212–233)	230[6]	186–212	–
Cx III	–	53 (43–60)	–	–	58 (54–63)	–	52–60	59 (59–60)	55 (50–61)	–	48–56	50–54
Tr III	–	–	–	–	35 (30–39)	–	34–40	42 (41–43)	35 (30–41)	–	36–40	30–40
Fe III	–	38 (35–45)	45	42–45	35 (32–37)	–	32–36	43 (35–51)	41 (38–48)	–	32–40	38–48
Ge III	–	13	15–16	15	11 (9–13)	–	12–16	15 (15–16)	16 (14–18)	–	14–16	14–16
Ti III	–	17 (15–20)	21	20–23	18 (17–21)	–	18–22	24 (24–25)	23 (18–26)	–	18–26	18–22
Ta III	–	32 (30–33)	50–55	45	23 (22–23)	–	44–48	30 (28–32)	26 (23–30)	–	52–56	40–50
Leg III	–	–	–	–	177 (169–181)	–	198–212	216 (210–222)	196 (181–208)	230[6]	210–216	
IP	–	–	–	–	–	–	664–732	752 (751–754)	695 (650–735)	750[6]	–	

[1]due to the condition of specimens from type series, the sample size for particular measurements varied (0–3 for *He. abirami*, 0–7 for *He. marittae*).
[2]rounded to integers (except for ratios); original data (Almada & Cédola (2017), Pérez-Espinoza & Moreno Salas (2016)) given with decimal values.
[3]measured with or without gnathosoma.
[4]provided twice (Almada & Cédola (2017: 1089), with different values.
[5]in *He. sorayae* (Q5 divided, plates not set apart) the actual width of Q5 s.hould equal half of the listed value.
[6]including claws.
[7]holotype and six paratypes from Sumatra; measurements of PLN, PLN3, PLN4, PLN5, based on one specimen, completed during present study.
[8]probably a mistake.

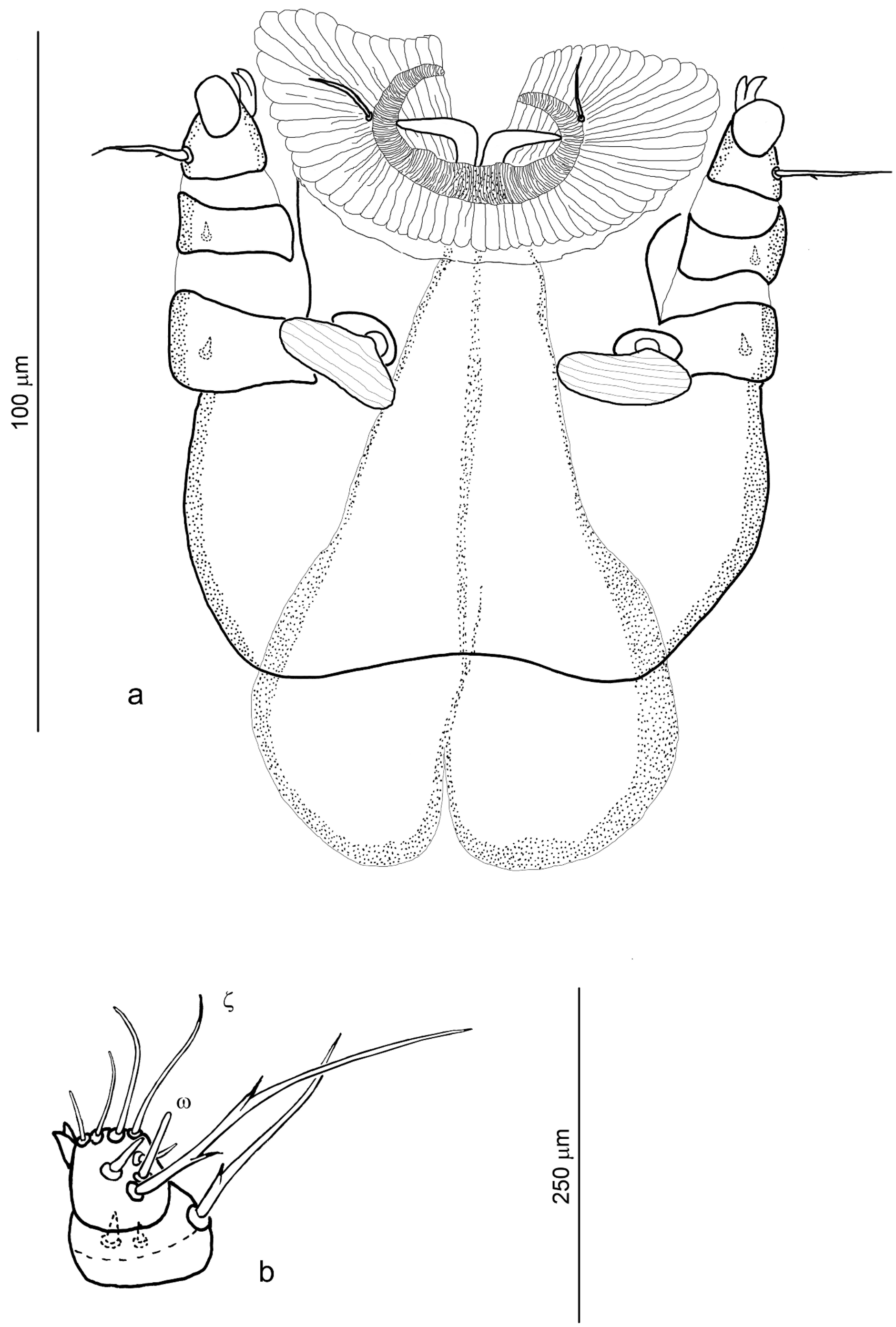

Figure 1. *Hexathrombium abirami*, larva. a) Gnathosoma (complete chaetotaxy of palp tibia and palp tarsus not shown). b) Details of palp tibia and palp tarsus.

Remarks. The new specimens collected in Peru and studied in this work were compared with the type material of *He. abirami*, and also with other species of *Hexathrombium*, with an emphasis on the South American species in the genus. A comparison of the metric data of the Peruvian specimens with the type series is included in Tables I and II. The differences observed in metric data between the type series of *He.*

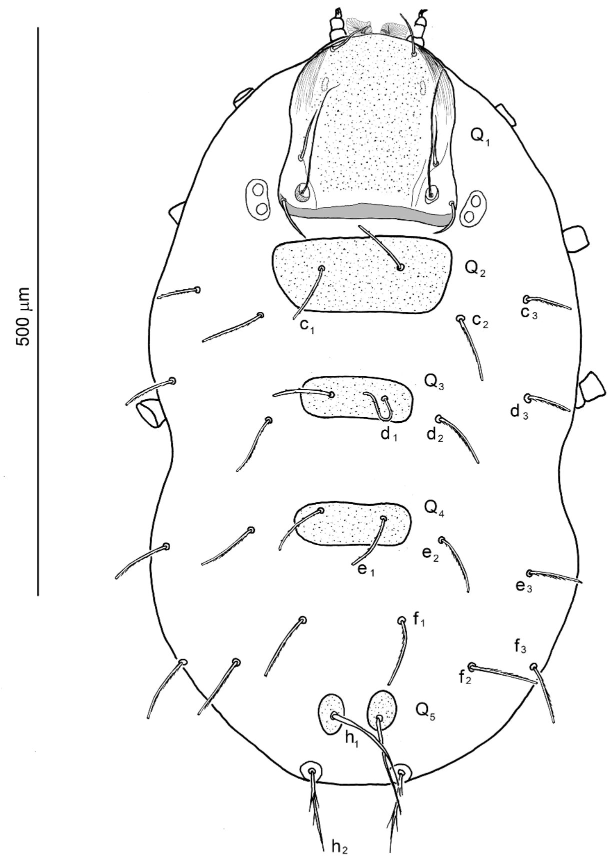

Figure 2. *Hexathrombium abirami*, larva. Idiosoma, dorsal aspect.

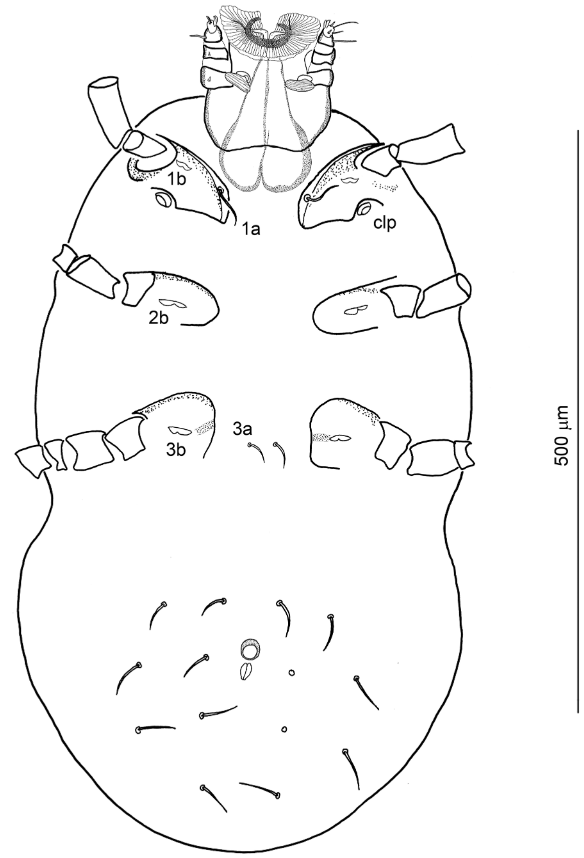

Figure 4. *Hexathrombium abirami*, larva. Gnathosoma and idiosoma, ventral aspect.

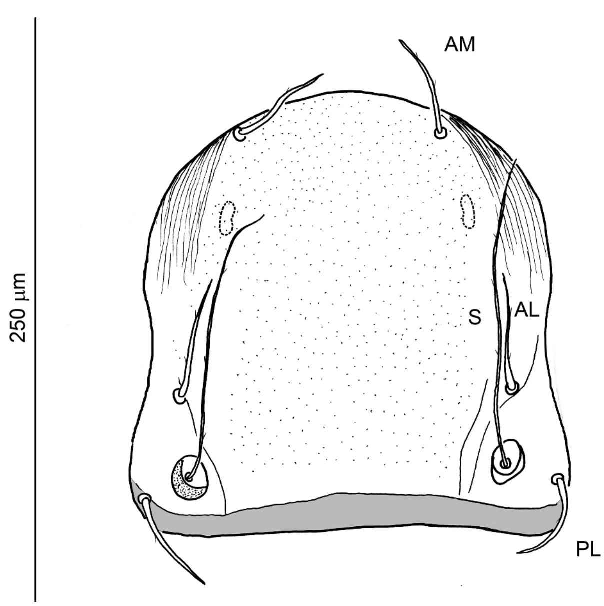

Figure 3. *Hexathrombium abirami*, larva. Scutum.

abirami and specimens collected in Peru (Table I) are attributed to intraspecific variations. These variations may be a result of the differences in geographic locations, ecological factors, and the mounting quality of the type material that may have affected the reliability of some measurements.

Based on the reexamination of the holotype and two paratypes of *He. abirami* Haitlinger, 1997, some characters redescribed here differ from those reported in the original description. A pair of eyes (each composed of two lenses placed on a common sclerite) are present at each side of scutum (original description, Figure 1, p. 82: one lens present at posterolateral margin of scutum, on each side of symmetry axis). Setae AL = 54 (original description: AL broken in all specimens); fn Fe = 6-5-4 (original description: fn Fe = 5-5-4); fn Ge = 5-2-2 (original description: fn Ge = 5-5-3); fn Ti = 6-5-5 (original description: fn Ti = 8-7-5); fsol Ti = 2-2-0 (original description: 2-1-0); vestigiala on tibia I, 2 eupathidia on tarsus I, famulus on tarsus II present. Preanal tubercle present.

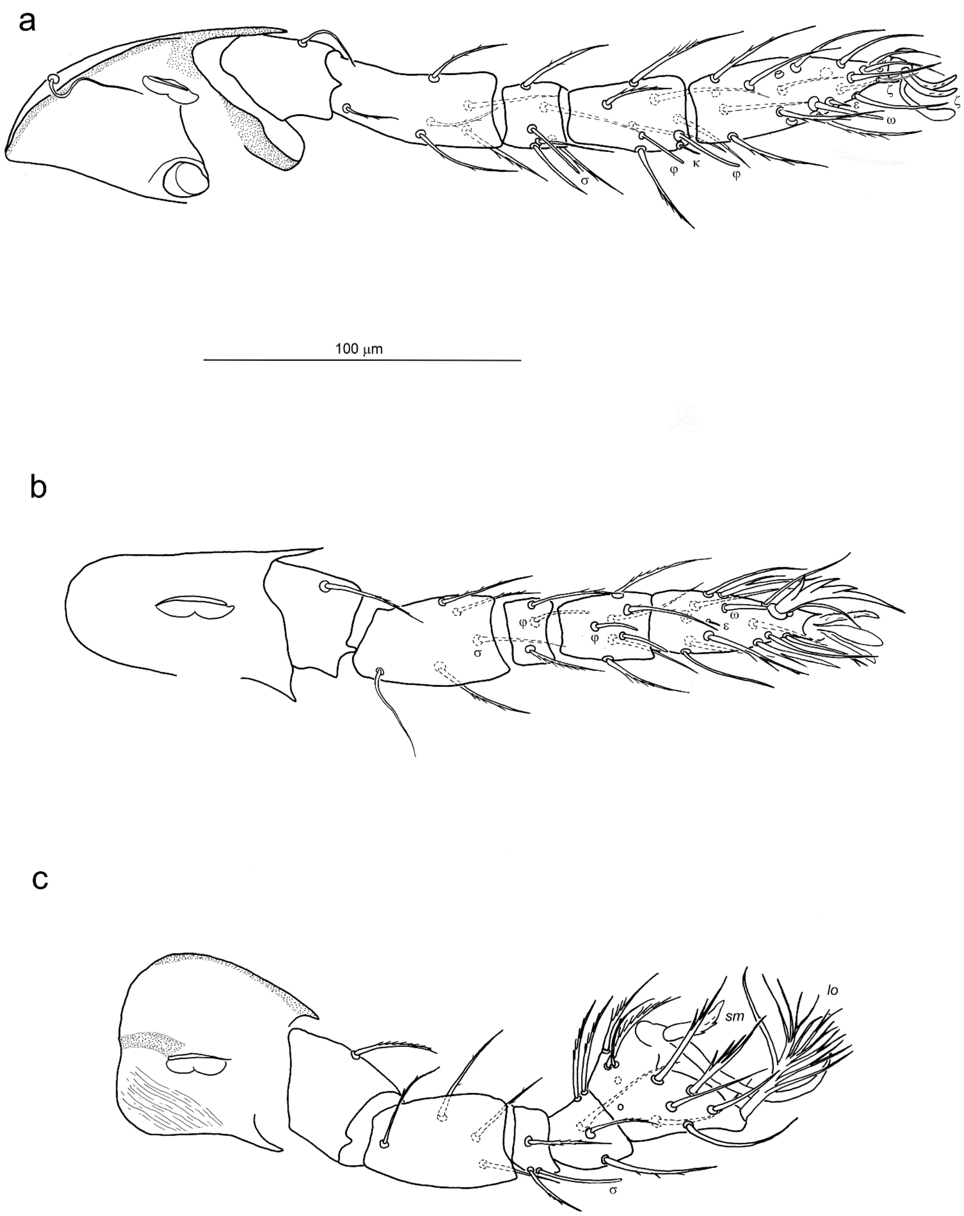

Figure 5. *Hexathrombium abirami*, larva. Legs (trochanter – tarsus). a) leg I. b) leg II. c) leg III. Abbreviations: *lo* – lophotrix, *sm* – smilum.

Parasitism of specimens collected in Peru. Altogether, 361 larvae were found parasitizing a single carabid host, *T. fulgida* (Figures 8(a–d) and 9(a–d)). Eight were attached to the head (including labrum) (Figure 8(a–d)), 86 to the pronotum (Figure 8(a)), 183 to the elytra (22 under elytra) (Figure 8(a) and 9(a),(c)), 50 to the thorax and venter of abdomen (Figures 8(a–d) and 9(b)), and 26 were distributed among various leg segments (Figure 9(d)); for the remaining eight larvae the attachment sites were not recorded. Parasites seem to show a preference for the dorsal parts of the host and there was no preference for softer cuticle areas (including the dorsal abdomen), and instead the preference was for externally exposed areas that seem to be out of the reach of the host legs. Larvae were relatively firmly attached, and except for eight specimens, the detachment had to be performed with an entomological pin and forceps.

Distribution. Neotropical (Brazil - original description, Peru - present data).

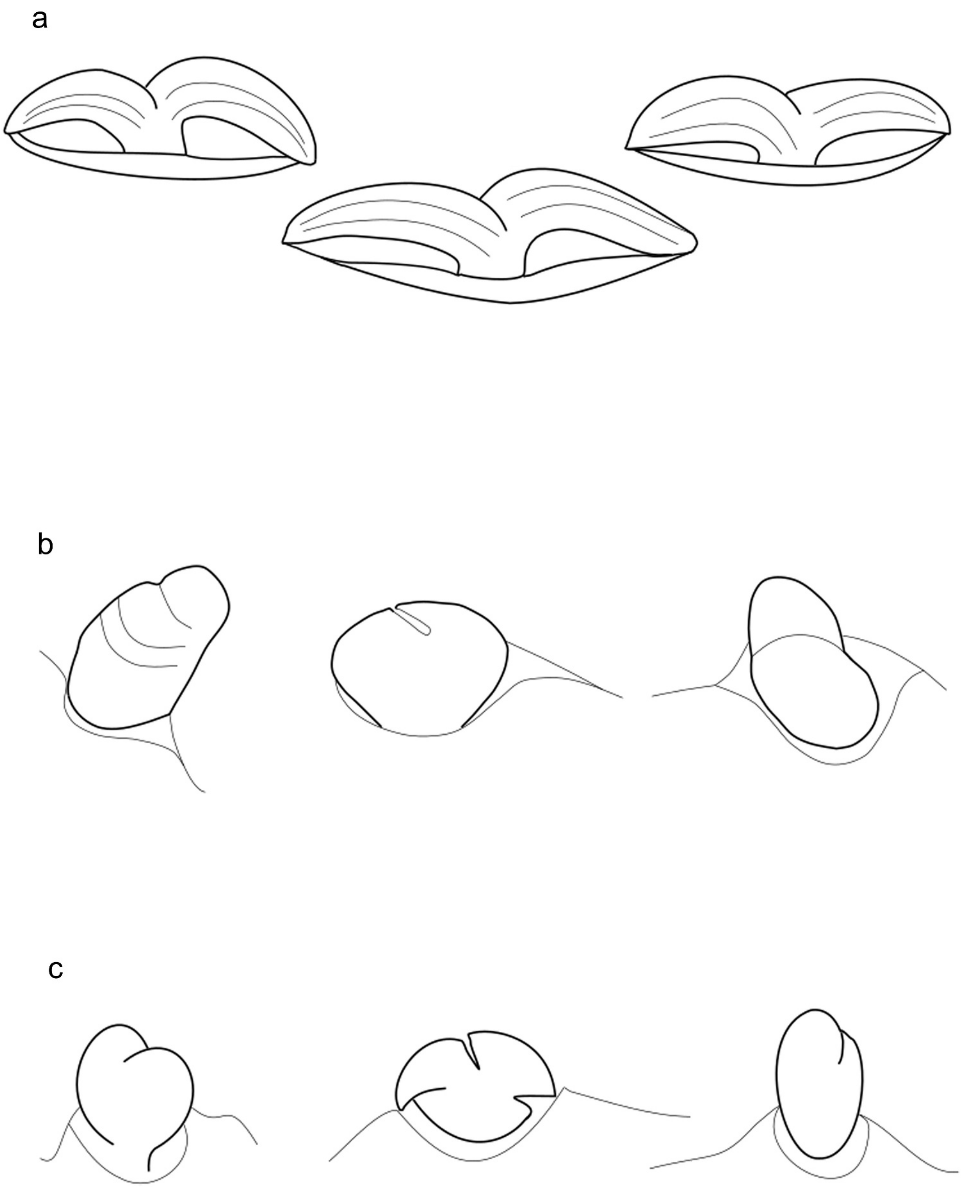

Figure 6. Lateral coxalae I (*1b*), II (*2b*), III (*3b*) in larvae of Hexathrombiini. a) *Hexathrombium abirami*, holotype. b) *Beronium veronicae*, holotype. c) *Alhamitrombium tetraseta*, holotype. Not to scale.

Supplementary data to the original descriptions of *He. lubomirae, He. mamerti* and *He. marittae*

Hexathrombium lubomirae (Haitlinger, 1994)

Beronium lubomirae Haitlinger, 1994: 50.
Hexathrombium lubomirae: Haitlinger 1997: 81.

Material examined. Holotype and six paratypes from Sumatra, mounted on one slide. For leg chaetotaxy see Table II.

Pygidial shield (Q5) undivided, with indistinct median incision at the posterior margin. Setae *1a* shifted beyond the margin of coxa. Setae *3a* absent. Setae *1b, 2b, 3b* as in *He. abirami*. Preanal tubercle present. fn Fe = 6-5-4 (original description: fn Fe = 5-5-4); fn Ge = 5-2-2 (original description: fn Ge = 5-3-3); fsol Ge = 1-1-1 (original description fsol Ge = 0-0-0); fκ Ti = 1-0-0 (original description: fκ Ti = 0-0-0); fζ Ta = 2-0-0 (original description: 0-0-0); fε Ta = 1-1-0 (original description: 1-0-0). Lophotrix two-branched, each branch with several bristles (Figure 7(b)).

Hexathrombium mamerti Haitlinger, 1999

Hexathrombium mamerti Haitlinger, 1999: 58.

Table II. Leg chaetotaxy of *Hexathrombium* spp.[1] Species with divided pygidial shield Q5: *He. abirami, He. fageli, He. mamerti, He. sorayae, He. southcotti*. Species with undivided pygidial shield: *He. marittae, He. lubomirae, He. willisi.*

	He. fageli Fain & Drugmand, 1993	*He. willisi* Southcott, 1993	*He. marittae* (Haitlinger, 1994)	*He. sorayae* (Haitlinger, 1994)	*He. lubomirae* (Haitlinger, 1994)	*He. abirami* Haitlinger, 1997	*He. abirami* Haitlinger, 1997	*He. southcotti* Zheng, 1997	*He. mamerti* Haitlinger, 1999
Source of data	Fain & Drugmand (1993)	Southcott (1993)[2]	Present study (type series)	Haitlinger (1994)	Present study (type material)	Present study (type material)	Present study (new material examined)	Zheng (1997)	Present study (type material)
Cx I	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with not widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, behind coxal plate, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]	2 [1a – normal, 1b – modified, with widely divergent lobes]
Tr I	1n	1n	1n	1n	1n	1n	1n	1n	1n
Fe I	6n	5–6n	6n	6n	6n	6n	6n	6n	6n
Ge I	4n, 2σ	[?]n, 2σ	[?]4n, 2σ	5n, 1σ	5n, 1σ	5n, 1σ	5n, 1σ	6n	5n, 1σ
Ti I	6n, 2φ	4n, 1φ	6n, 2φ, 1κ	6n, 2φ, 1κ	6n, 2φ, 1κ	6n, 2φ, 1κ	6n, 2φ, 1κ	8n[4]	6n, 2φ, 1κ
Ta I	[?]n, 1ω, 1ζ, 1ε	[?]14n, 1ω	[?]18n, 1ω, [?] 2ζ[3], 1ε	[?]16n, 1ω, 1ε	*c.* 16n, 1ω, 2ζ, 1ε	[?]15n, 1ω, [?] 2ζ[3], 1ε	18n, 1ω, 2ζ, 1ε	19n	[?]16n, 1ω, 2ζ, 1ε
Cx II	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with not widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]	1 [2b – modified, with widely divergent lobes]
Tr II	1n	1n	1n	1n	1n	1n	1n	1n	1n
Fe II	5n	5n	5n	5n	5n	5n	5n	5n	5n
Ge II	2n, 1σ	[?]n, 1σ	3n	3n	2n, 1σ	2n, 1σ	2n, 1σ	4n	2n, 1σ
Ti II	5n, 2φ	6n, 1φ	6n	5n, 2φ	5n, 2φ	5n, 2φ	5n, 2φ	7n[5]	5n, 2φ
Ta II	[?]n, 1ω	[?]11n, 1ω	14n, 1ω	13n, 1ω	*c.*13n, 1ω, 1ε	[?]14n, 1ω, 1ε	14n, 1ω, 1ε	15n	[?]12n, 1ω, 1ε
Cx III	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with not widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]	1 [3b – modified, with widely divergent lobes]
Tr III	1n	1n	1n	1n	1n	1n	1n	1n	1n
Fe III	4n	4n	4n	4n	4n	4n	4n	3n	4n
Ge III	2n, 1σ	[?]n, 1σ	2n, 1σ	3n[7]	2n, 1σ	2n, 1σ	2n, 1σ	3n[6]	2n, 1σ
Ti III	5n	5n	5n	5n	5n	5n	5n	4n	5n
Ta III	[?]n	[?]9n	[?]10n	*c.* 10n	*c.* 11n	*c.* 11n	11n	14n	[?]12n

[1]*He. cicindelae* and *He. spatuliferum* omitted due to the unavailability of data.
[2]data on *He. willisi* incomplete (see Southcott 1993), partly inferred from drawing.
[3]the presence of eupathidia on tarsi difficult to ascertain based on type material examined.
[4]the state 6n, 2φ or 6n, 2φ, 1κ cannot be excluded.
[5]the state 5n, 2φ cannot be excluded.
[6]the state 2n, 1σ cannot be excluded.

Table III. Meristic traits related to idiosoma of *Hexathrombium* spp. Species with divided pygidial shield Q5: *He. abirami, He. cicindelae, He. fageli, He. mamerti, He. sorayae, He. southcotti*. Species with undivided pygidial shield: *He. marittae, He. lubomirae*. For *He. willisi* see Southcott (1993).

	He. cicindelae (Floch & Abonnenc, 1941)	*He. fageli* Fain & Drugmand, 1993	*He. spatuliferum* Cooreman, 1944	*He. marittae* (Haitlinger, 1994)	*He. sorayae* (Haitlinger, 1994)	*He. lubomirae* (Haitlinger, 1994)	*He. abirami* Haitlinger, 1997	*He. southcotti* Zheng, 1997	*He. mamerti* Haitlinger, 1999
Source of data	Floch & Abonnenc (1941)	Fain & Drugmand (1993)	Cooreman (1944)	Present study (type material)	Haitlinger (1994)	Haitlinger (1994)	Present study (type material and new material examined)	Zheng (1997)	Haitlinger (1999)
fV	14[1]	16	16[2]	14	14[3]	12(14)	14	18–20	14

[1]the presence 18 setae (including [?]*3a* and h2 stated in the original description by Floch & Abonnenc (1941); 14 setae present in *He. cf. cicindelae* by Almada & Cédola (2017) (one extra pair should be assigned to dorsal formula).
[2]setae h_2 drawn by Cooreman (1944) on ventral face of idiosoma should be excluded from fV formula.
[3]the presence of 12 setae reported by Haitlinger (1994) in the text and 14 setae (none of which is duplicated in the dorsal formula) provided in the drawing.

Table IV. Host and distribution data on *Hexathrombium* spp. recorded from South America.

	He. cicindelae (Floch & Abonnenc, 1941)	*He. cf. cicindelae*	*He. marittae* (Haitlinger, 1994)	*He. cf. marittae*[1]	*He. abirami* Haitlinger, 1997	*He. abirami* Haitlinger, 1997
Host	Coleoptera Carabidae *Odontocheila cajennensis* (Fabricius)	Coleoptera Carabidae *Tetracha* (*Tetracha*) *brasiliensis brasiliensis* (Kirky)	Coleoptera Carabidae *Ceroglossus buqueti sybarita* Gerstaecker, *Ceroglossus darwini* Fabricius, *Ceroglossus suturalis* Hoppe, [?] *"Ceroglossus valdiviae* Hoppe*"*	Coleoptera Carabidae *Ceroglossus buqueti* (Laporte)	Coleoptera Erotylidae Undetermined Erotylidae	Coleoptera Carabidae *Tetracha fulgida* (Klug)
Distribution in South America	French Guiana	Argentina	Chile	Chile	Brazil	Peru
References	Floch & Abonnenc (1941), Felska et al. (2018)	Almada & Cédola (2017)	Haitlinger (1994), Felska & al. (2018)	Pérez-Espinoza & Moreno Salas (2016)	Haitlinger (1997)	This study

[1]according to Pérez-Espinoza & Moreno Salas (2016) the length of setae, used as diagnostic character, is highly variable, and measures of QL setae do not correspond with the key; however, measures of setae QL5, AP and MA, correspond to the description of *He. marittae* by Haitlinger (1997).

Material examined. Holotype and eight paratypes mounted on one slide. For leg chaetotaxy see Table II.

Setae *1b, 2b, 3b* as in *He. abirami*. fn Fe = 6-5-4 (original description: fn Fe = 5-5-4); fκ Ti = 1-0-0 (original description: fκ Ti = 0-0-0); fζ Ta = 2-0-0 (original description: 0-0-0); fε Ta = 1-1-0 (original description: 0-0-0). Tarsus I, tarsus II and femur III bearing a distinct seta, smooth or with few short barbs, much longer than the other setae in the segment. Lophotrix composed of two branches; the most proximal branch bifurcate at termination. The distal branch of the stem with several (*c.* 5) secondary branches (at least three of those as well as the main stem are bifurcate at termination (Figure 7(c)).

This species is similar to *He. abirami*, however it shows smaller measurements for most of the characters studied (see Table I).

Hexathrombium marittae (Haitlinger, 1994)

Beronium marittae Haitlinger, 1994: 48.
Hexathrombium marittae: Haitlinger 1997: 81.

Material examined. Holotype and four paratypes mounted on one slide and collected from *Ceroglossus sybarita* (now *Ceroglossus buqueti sybarita*); two paratypes mounted on another slide and

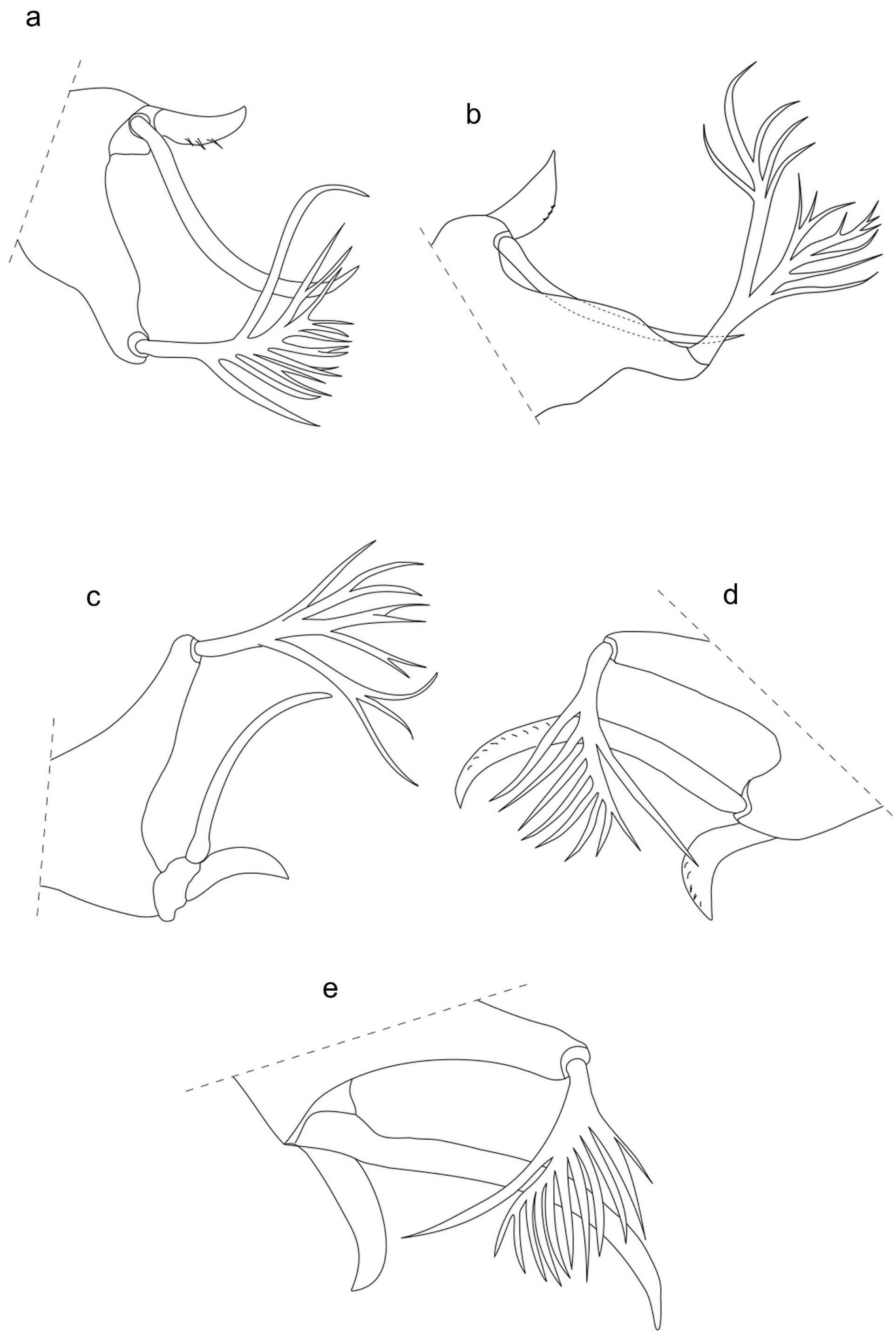

Figure 7. Lophotrix in larvae of Hexathrombiini. a) *Hexathrombium abirami*. b) *Hexathrombium lubomirae*, holotype. c) *Hexathrombium mamerti*. d) *Beronium veronicae*, holotype. e) *Alhamitrombium tetraseta*, holotype. Not to scale.

collected from *Ceroglossus darwini*. Metric data are shown in Table I. For leg chaetotaxy see Table II.

Pygidial shield (Q5) undivided. fV = 14 (original description: fV = 20). Preanal tubercle present. Distal part of tarsus II with a fan-like seta, similar to one observed in *He. abirami*, but less robust.

Hoplothrombium **Ewing, 1925**

Hoplothrombium Ewing, 1925: 263.
Hoplothrombium: Vercammen-Grandjean 1967: 2.

Diagnosis (after Vercammen-Grandjean 1967).

Larva. The posterior-most shield on idiosoma dorsum (pygidial shield, Q5) oblong, undivided.

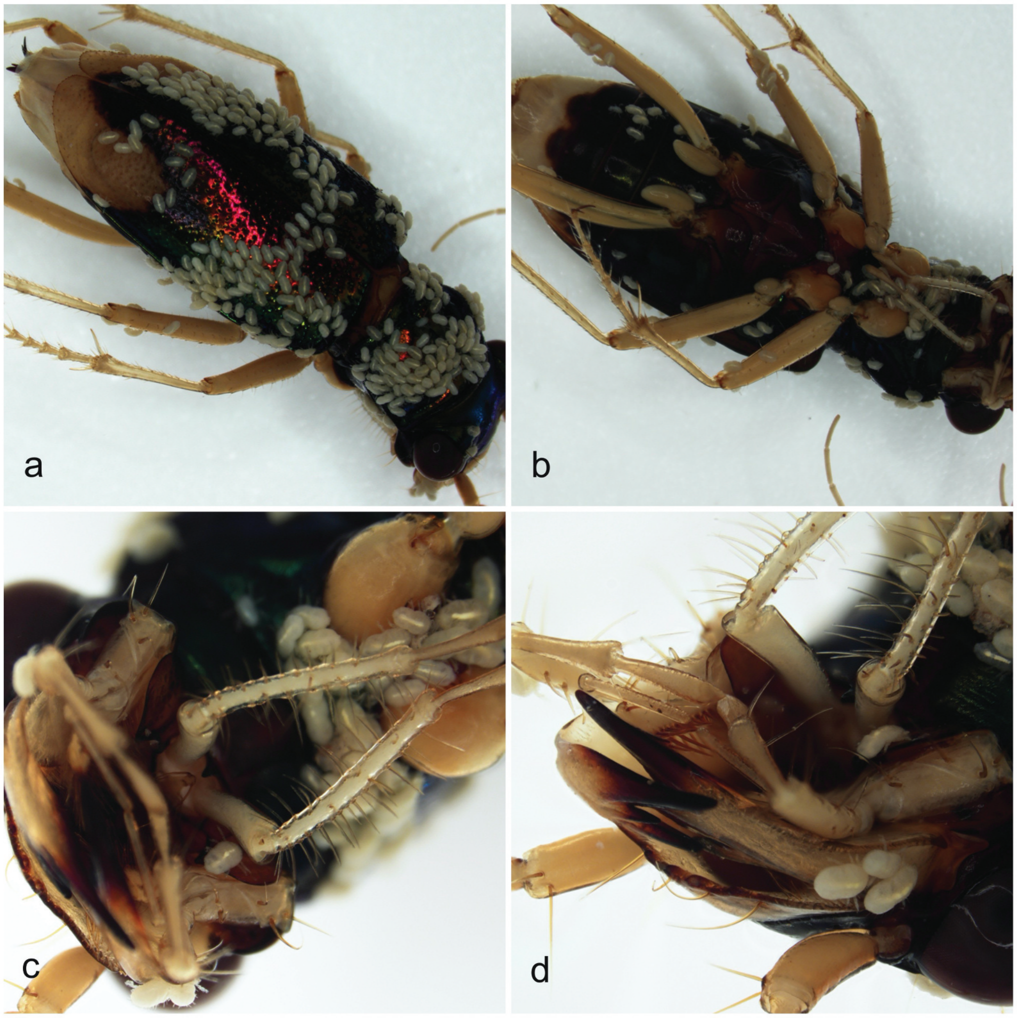

Figure 8. *Tetracha fulgida* with larvae of *Hexathrombium abirami*. a) dorsal habitus of the host. b) ventral habitus. c) head and anterior part of thorax, ventral view. d) head and anterior part of thorax, side view. Not to scale.

Eye composed of one lens inserted in an elongate ocular plate. Odontus simple. fCx = 2-2-2. Medial coxala I (*1a*) simple, elongate, smooth. Lateral coxala I (*1b*), medial and lateral coxala II (*2a, 2b*) and lateral coxala III (*3b*) spike-like. Medial coxala III (*3a*) barbed. fV = 18. Hypostomala in the form of a thick, short spine.

Type species. *Hoplothrombium quinquescutatum* Ewing, 1925

Species included and country record. *Ho. quinquescutatum*, Canada.

Hosts. [?] Oribatida (Ewing 1925).

Beronium Southcott, 1986

Beronium Southcott, 1986: 62.

Diagnosis (after Southcott 1986; Haitlinger 1994; Mayoral & Barranco 2005b, verified).

Larva. The posterior-most shield on idiosoma dorsum (pygidial shield, Q5) oblong, undivided. Eye lenses absent, ocular plate elongate. Odontus bifid. fCx = 2-1-1. Medial coxala I (*1a*) simple, thickened in anterior half, then acuminating or short, thin, setulose. Lateral coxala I (*1b*) short, stout either with blunt end or indistinctly bifid at termination, sometimes amorphic in anterior part. Lateral coxala II (*2b*) short, stout with rounded ends, slightly bifid. Coxala III (*3b*) short, peg-like, unilobed or indistinctly bifid. Setae *3a* absent. Pre-anal tubercle present. fV 18–23. Setae around anal slit short, slightly thickened or thick, spine-like. Hypostomala reniform.

Type species. *Hoplothrombium coiffaiti* Beron, 1973

Figure 9. *Tetracha fulgida* with larvae of *Hexathrombium abirami*. a) elytra. b) venter of abdomen. c) elytra (close-up). d) leg. Not to scale.

Species included and country records. *B. coiffaiti*, Morocco; *B. veronicae*, Spain (Canary Islands); *B. laemostenis*, Spain.

Hosts. Coleoptera: Carabidae (Platyninae: Sphodrini: Sphodrina).

Remarks. The absence of eyes, hitherto reported for *Beronium*, constitutes one of the main differences which allow to distinguish between *Beronium* spp., *Alhamitrombium*, spp. and *Hexathrombium* spp. In *B. laemostenis* and *B. veronicae*, ocular sclerites are present and they are elongated in shape, narrowing anteriorly and truncated posteriorly (Figure 10(a)); they are located adjacent to the posterolateral margins of the scutum, and in a similar location to the ocular plates observed in other trombidioid genera (including *Hexathrombium*). The plates are punctated over the entire surface and surrounded by folded in lines cuticle. The shape of these sclerotized structures resembles the plates surrounding the eye lenses in *Hoplothrombium* (Vercammen-Grandjean 1967: 5).

Beronium veronicae **Haitlinger, 1994**

Beronium veronicae Haitlinger, 1994: 50.

Material examined. Holotype and two paratypes mounted on one slide. For leg chaetotaxy see Table II.

Supplementary data to the original description of *B. veronicae*: pre-anal tubercle present (Figure 10(b)); coxalae *1b* and *2b* short, thick, indistinctly bifid, rounded lobes; coxalae *3b* unilobed, peg-like and rounded terminally; fsol Ge = 1-1-1 (original description fsol Ge = 1-1-0). Setae on legs distinctly setulated. Lophotrix composed of two branches diverging from

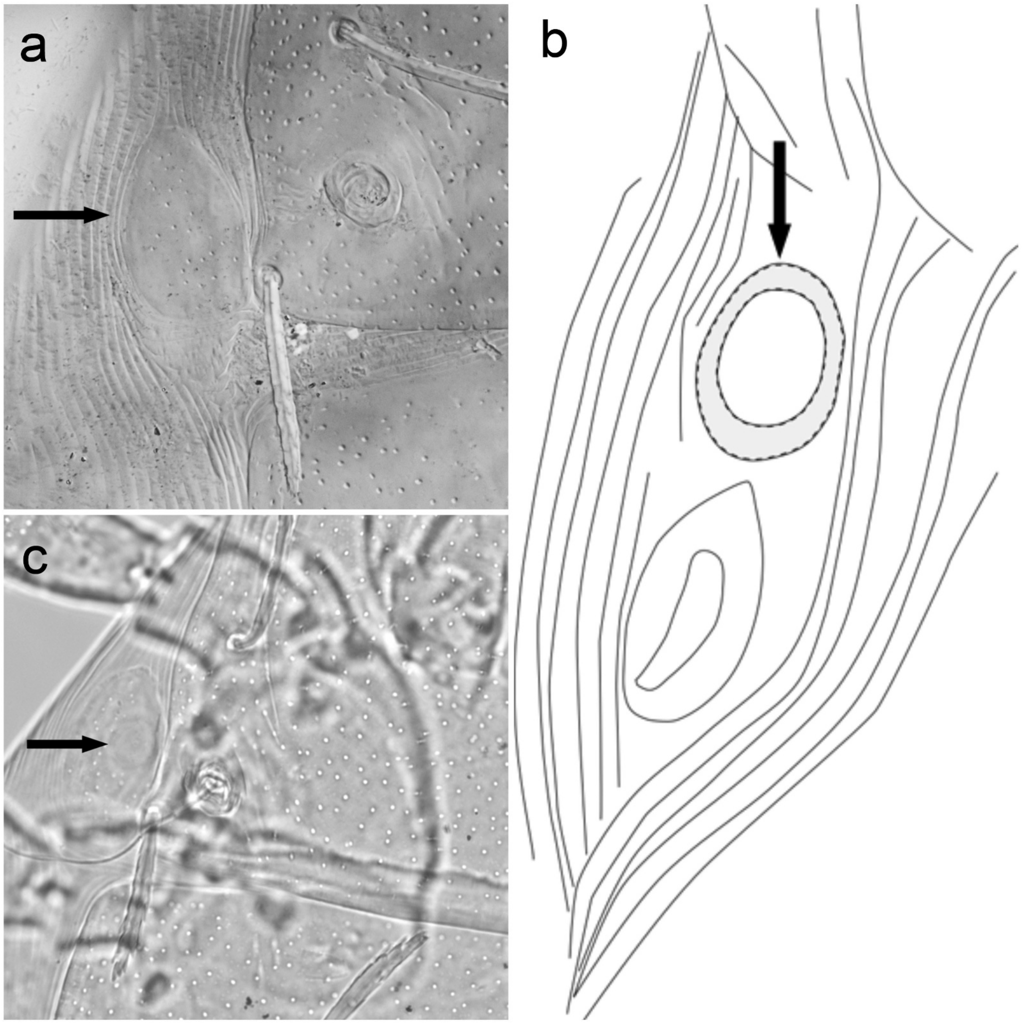

Figure 10. *Beronium veronicae*, holotype, larva. a) ocular sclerite. b) preanal tubercle. *Alhamitrombium tetraseta*, holotype, larva. c) ocular sclerite. Not to scale.

the main stem; one branch nude, the other one with several (*c.* 7) secondary branches (Figure 7(d)).

Mayoral & Barranco (2005b) in their key to *Beronium* spp., and followed by Mayoral (2013), referred to the presence of one solenidion on genu I and the lack of solenidia on genu III as characters to differentiate *B. veronicae* from the other two species in the genus. This was based on the original description of *B. veronicae*, in which Haitlinger (1994) described one solenidion on genu I and no solenidia on genu III. The present reexamination of the type material of *B. veronicae* allowed to confirm the presence of one solenidion on Ge I, but there is also a solenidion present on Ge III. Therefore, the presence of one solenidion on genu III should be treated as character shared by all three species assigned to *Beronium*. It is still possible to separate *B. laemostenis* from *B. veronicae* based on the number of solenidia on Ge I (2 *vs.* 1) (see Table V). Future reexamination of *B. coiffaiti* should help to verify the taxonomic status of this species.

The leg chaetotaxy of all three nominal species assigned to the genus is provided in Table V. The differences between the members of *Beronium* may pertain also to the number of setae in fV formula (*B. coiffaiti* – 19, *B. laemostenis* – 18–23, *B. veronicae* – 22(23)).

***Alhamitrombium* Mayoral & Barranco, 2005**

Alhamitrombium Mayoral & Barranco, 2005a: 111.

Diagnosis (after Mayoral & Barranco 2005a, verified).

Larva. The posterior-most shield on idiosoma dorsum (pygidial shield, Q5) entire, oblong. Eye composed of one lens inserted in elongate ocular plate (Figure 10(c)). Odontus bifid. fCx = 2-1-1.

Medial coxala I (*1a*) long, simple, slender. Lateral coxala I (*1b*) short, stout, distinctly bilobed, coxala II (*2b*) bilobed, with diverged rounded processes (fan-like), and coxala III (*3b*) short, peg-like, unilobed (Figure 6(c)). Setae *3a* absent. fV = 21–23. Setae around anal slit long, robust, tapering and similar to *1a* setae. Pre-anal tubercle present. Hypostomala reniform. Lophotrix composed of a main branch with 9 smaller secondary branches that shorten gradually towards distal end; a secondary long branch without ramifications is located anteriorly (Figure 7(e)).

Type species. Alhamitrombium tetraseta Mayoral & Barranco, 2005

Species included and country record. A. tetraseta, Spain.

Hosts. Coleoptera: Carabidae (Harpalinae: Lebiini).

Key to *Hexathrombiini* genera

[incl. *Hoplothrombium* - monotypic, *Alhamitrombium* - monotypic, *Beronium, Hexathrombium*]

Modified from Southcott 1993; Haitlinger 1994; 1997; Mayoral & Barranco 2005a, 2005b and based on the type material and material examined in this study (see: Material and methods)

1. fCx 2-2-2; lateral coxala I (*1b*) not modified, simple .... *Hoplothrombium* [*Ho. quinquescutatum*]
- fCx 2-1-1; lateral coxala I (*1b*) modified, stout, peg-like or bifid 2
2. seta *3a* absent; coxala III (*3b*) not bifid, with rounded or only indistinctly incised termination 3
- seta *3a* present or absent; coxala III (*3b*) bifid, with diverging or adjacent to each other processes .... *Hexathrombium* [for the selection of species see provisional key below]
3. one eye on each side of prodorsum; ocular plate present; medial coxala (*1a*) slender, setulose, lateral coxala I (*1b*) stout, bilobed .... *Alhamitrombium* [*A. tetraseta*]
- eyes absent; ocular plate present; medial coxala (*1a*) simple, lateral coxala I (*1b*) stout, indistinctly bifid or blunt .... *Beronium* [*B. coiffaiti, B. laemostenis, B. veronicae*]

Provisional key to *Hexathrombium* species

1. setae *3a* present between coxal plates III [*He. abirami, He cicindelae, He. fageli, He. mamerti, He. southcotti, He. spatuliferum, He. willisi*] 2

Table V. Leg chaetotaxy of *Beronium* spp.

	B. coiffaiti (Beron, 1973)	*B. laemostenis* Mayoral & Barranco, 2005	*B. veronicae* Haitlinger, 1994
Source of data	Beron (1973)	Mayoral & Barranco (2005b) and present study (type material)	Present study (type material)
Cx I	2 [1a – simple, 1b – modified, short, thick, indistinctly bifid]	2 [1a – simple, 1b – modified, short, thick, indistinctly bifid]	2 [1a – simple, 1b – modified, short, thick, indistinctly bifid]
Tr I	1n	1n	1n
Fe I	6n	6n	6n
Ge I	6n	4n, 2σ	5n[1], 1σ
Ti I	8[2]	7n, 2φ, 1κ	6n, 2φ, 1κ
Ta I	16n, 1ω, 1ε[3]	20n, 1ω, 1ε	*c.* 16n, 1ω, 2ζ, 1ε
Cx II	1 [2b – modified, indistinctly bifid]	1 [2b – modified, short, bifid]	1 [2b – modified, indistinctly bifid]
Tr II	1n	1n	1n
Fe II	5n	5n	5n
Ge II	3n[4]	2n, 1σ	2n, 1σ
Ti II	7[5]	5n, 2φ	5n, 2φ
Ta II	12n, 1ω	14n, 1ω, 1ε	*c.* 16n, 1ω, 1ε
Cx III	1 [3b – modified, indistinctly bifid]	1 [3b – modified, peg-like, unilobed]	1 [3b – modified, indistinctly bifid]
Tr III	1n	1n	1n
Fe III	4n	4n	4n
Ge III	2n, 1σ	2n, 1σ	2n, 1σ
Ti III	5n	5n	5n
Ta III	11n	14n	*c.* 11n

[1]there are two setae which are smooth and their actual nature is difficult to ascertain.
[2]a total of eight setae reported by Beron (1973); the state 6n, 2φ cannot be excluded.
[3]presence of famulus inferred from the drawing provided by Beron (1973).
[4]the state 2n, 1σ cannot be excluded.
[5]a total of seven setae reported by Beron (1973); the state 5n, 2φ cannot be excluded.

-. setae *3a* absent [*He. lubomirae, He. marittae, He. sorayae*] 6
2. coxalae *1b, 2b, 3b* with pointed, widely divergent lobes; pygidial shield (Q5) divided into two separate plates, each encompassing the base of one h_1 seta [*He. abirami, He. cicindelae, He. fageli, He. mamerti, He. southcotti, He. spatuliferum*] 3
-. coxalae *1b, 2b, 3b* with rounded, not widely divergent lobes; pygidial shield (Q5) undivided, encompassing the bases of paired h_1 setae .... *He. willisi* [USA, Oklahoma]
3. elongate, needle-shaped seta, much longer than other leg setae, present on tarsus I, tarsus II and femur III .... *He. mamerti* [Australia]
-. elongate, needle-shaped seta absent .... [*He. abirami, He. cicindelae, He. fageli, He. southcotti, He. spatuliferum*] 4
4. leg setae setulated *He. fageli* [Ethiopia, Ivory Coast]
- leg setae barbed or nude .... [*He. abirami*, [?]*He. cicindelae*, [?]*He. southcotti, He. spatuliferum*] 5
5. setae PL levelled with S ..... *He. southcotti* [China]
-. setae PL posterior of S .... [*He. abirami* [Brazil, Peru], [?]*He. cicindelae**, *He. spatuliferum**]
6. pygidial shield (Q5) undivided, at most with medial incision at posterior border ..... [*He. lubomirae, He. marittae*] 10
pygidial shield (Q5) divided . *He. sorayae* [China]
7. pygidial shield oblong; AP > 50; QL5 < 100 .... *He. marittae* [Chile]
-. pygidial shield incised posteriorly; AP < 35; QL5 > 100 ... *He. lubomirae* [Madagascar, Sumatra]

**He. cicindelae* [French Guiana] excluded from further key identification due to the insufficiency of data provided in the description; *He. spatuliferum* [Zaire]– re-examination of type necessary.

Discussion

Fain and Drugmand (1993) and Southcott (1993) erected, independently and within the same year (1993), the tribe Hexathrombiini within Eutrombidiinae to accommodate *Beronium, Hexathrombium* and *Hoplothrombium*. Due to the time coincidence, the authorship of the tribe has been assigned by different authors to either Fain and Drugmand (Fain & Jocqué 1996) or Southcott (Mayoral & Barranco 2005a). Fain and Drugmand published their paper on September 10th, 1993, and Southcott's paper was published on October 1st, 1993. In accordance with the Article 24 and 50.6 of the International Code of Zoological Nomenclature (1999), we attribute the authorship of the tribe to Fain and Drugmand (1993); thus, Hexathrombiini Southcott, 1993 become an objective synonym of Hexathrombiini Fain & Drugmand, 1993.

Members of *Hexathrombiini* display relatively high consistency of character states, however the few differences observed at intratribal level seem to justify the independent status of genera hitherto assigned to this tribe. Among them, the presence/absence of eyes and the shape of coxal setae *1b, 2b, 3b* (see also Figures 6 and 10(a,c)) are particularly important. On the other hand, a limited number of differences between nominal species assigned to *Hexathrombium* and *Beronium* poses the question of the actual species borders. This is accentuated by the limited number of known species for each of these two genera. The answer to the question should be reconsidered in the future when more species are described, taking in consideration larvae, active postlarval forms and molecular results when they are available. The status of the species assigned to *Hexathrombium*, with special reference to South American and African members, should be revised in the future when the redescriptions of *He. cicindelae* and *He. spatuliferum* become available.

The functional significance of pre-anal tubercle in Hexathrombiini should be elucidated. The presence of this structure, referred by Southcott (1993) as a "*small near-circular structure*", was confirmed in the species *He. willisi, He. cf. marittae* and *He. cf. cicindelae* in *Hexathrombium* (Southcott 1993; Pérez-Espinoza & Moreno Salas 2016; Almada & Cédola 2017) and also in the species *A. tetraseta, B. laemostenis* and *B. veronicae* (see also Figure 10 (b)) during our reexamination of these type specimens. The tubercle, due to its overall small size, may have been overlooked by some authors and thus omitted in their descriptions.

In *Beronium* Southcott, 1986, the shape of coxal setae, especially *1b*, has been variously reported and there seems to be some variability in between specimens and species. Mayoral & Barranco (2005b) reported the presence of blunt and conical lateral coxala I in *Beronium*. In the current revision of the type material of *B. laemostenis*, it was possible to observe that there is some variation in the shape of this character among specimens. In this species, *1b* seta is mostly thick and conical, but some specimens show a deformation of the seta and in some others, it looks slightly bifid. Haitlinger (1994) did not describe the seta *1b* in *B. veronicae*, (except for referring to it as "thick seta") but in the present re-examination of the holotype we can confirm the presence of *1b* which is indistinctly bifid at termination (Figure 6(b)). This character (seta *1b*) should be verified in *B. coiffaiti*, that according to the description of Beron (1973) is dilated.

There are very little data available about the biology and ecology of Hexathrombiini. The infestation of the bright metallic tiger beetle (*T. fulgida*) by the parasitic mite larvae *He. abirami* may have taken place on the ground – in wet sand or mud – with sparse or no vegetation. This is the natural habitat of adults of *T. fulgida*. Remarkably, this beetle has been proposed as a natural predator of the pest mole cricket in golf courses (*T. fulgida* in GBIF 2019). The number of mite larvae recorded (361) on a single host specimen reported in this study is the highest number of parasites recorded in arthropod-associated terrestrial Parasitengona mites. The next two highest values reported were also recorded for Eutrombidiinae larvae. Severin (1944) reported the presence of 175 larvae of *Eutrombidium locustarum* on *Dissosteira carolina* (Orthoptera), and Pérez-Espinoza & Moreno Salas (2016) reported 186 larvae of *He. cf. marittae* infesting *Ceroglossus buqueti* (Coleoptera: Carabidae). The preferred attachment site of *Hexathrombium* spp. larvae varied across different hosts, despite the similarities in the hosts' body (they are closely related species). Around 50% of larvae collected in this study were attached to elytra. No larvae were attached to dorsal abdomen, which is consistent with the observations of Pérez-Espinoza and Moreno Salas (2016). Almada and Cédola (2017) reported that most larvae displayed a preference for the ventral thorax; in our study, only around 14% of larvae were attached to the thorax and venter abdomen.

Several morphological traits (presence of stephanostome facilitating a firm attachment to the host, relatively short legs), behavioral (preference to attachment sites with lower accessibility to hosts' legs) and ecological (relatively narrow host spectrum) are of significant adaptive advantage and may reflect the relatively long co-evolution of *Hexathrombium* and other Hexathrombiini with their hosts.

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Authors' contributions

JMąkol and JMayoral contributed to the study design. SF performed the collection of *T. fulgida* with parasitic mites as well as the morphological identification of the host species. JMąkol performed the morphological analyses of new material of *Hexathrombium* collected from Peru and type material of *Hexathrombium* spp. and *B. veronicae*. JMayoral examined the type material of *B. laemostenis* and *Alhamithrombium*. JMąkol and JMayoral wrote the manuscript. All authors reviewed, read and approved the manuscript.

Availability of data and material

All data generated or analysed during this study are included in this published article. The type material examined has been loaned from museum institutions. The non-type material of *Hexathrombium abirami* collected from Peru along with host specimen is stored in the collection of the Department of Invertebrate Systematic and Ecology, Wrocław University of Environmental and Life Sciences, Poland.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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References

Almada MS, Cédola C. 2017. First record of *Hexathrombium* (Acari: Microtrombidiidae) on *Tetracha* (*Tetracha*) *brasiliensis brasiliensis* (Coleoptera: Cicindelidae) in Argentina. Systematic and Applied Acarology 22(7):1087–1090. DOI:10.11158/saa.22.7.15.

Beron P. 1973. Une nouvelle larve d'Acarien (*Hoplothrombium coiffaiti* sp.n., Trombidiidae) parasite d'un Coleoptere cavernicole du Maroc. Annales de Spéléologie 3:413–416.

Cooreman J. 1944. Notes et observations sur les Acariens III. Bulletin du Musée royal d'histoire naturelle de Belgique 20:1–16.

Ewing HE. 1925. A contribution to our knowledge of the taxonomy of chiggers including the descriptions of a new genus, six new species and a new variety. The American Journal of Tropical Medicine 5:251–265. DOI:10.4269/ajtmh.1925.s1-5.251.

Fain A, Drugmand D. 1993. Notes on the genus *Hexathrombium* Cooreman 1944 (Acari, Trombidiidae) with description of a new tribe and species from afrotropical Staphylinidae (Coleoptera). Bulletin et annales de la Société royale belge d'entomologie 129:121–128.

Fain A, Jocqué R. 1996. A new genus and species of larval Eutrombidiinae Thor, 1935 (Acari: Microtrombidiidae) from an afrotropical spider. International Journal of Acarology 1:11–16. DOI: 10.1080/01647959608684075.

Felska M, Wohltmann A, Mąkol J. 2018. A synopsis of host-parasite associations between Trombidioidea (Trombidiformes: Prostigmata, Parasitengona) and arthropod hosts. Systematic and Applied Acarology 23(7):1375–1479. DOI:10.11158/saa.23.7.14.

Floch H, Abonnenc E. 1941. Trombidides de la Guyana Francaise. Le "pou d'agouti". Archives de l'Institut Pasteur de la Guyane Française et du Territoire de l'Inini 20:1–22.

Haitlinger R. 1994. Four new larval mites (Acari: Trombidiidae: Eutrombidiinae) ectoparasitic on carabids (Insecta: Coleoptera: Carabidae). Revista Chilena Entomologia 21:47–56.

Haitlinger R. 1997. A new species of *Hexathrombium* Cooreman 1944 based on parasitic larva on erotylids from Brazil (Acari: Eutrombidiidae). Memórias Do Instituto Oswaldo Cruz 92:81–83. DOI:10.1590/S0074-02761997000100015.

Haitlinger R. 1999. Three new larval mites (Acari: Prostigmata: Eutrombidiidae, Erythraeidae, Trombellidae) from Australia, Turkey and Thailand. Zeszyty Naukowe Akademii Rolniczej We Wrocławiu, Zootechnika XLV 362:57–73.

Husband RW, Wohltmann A. 2011. A redescription of *Eutrombidium locustarum* (Walsh) (Acari: Microtrombidiidae) and a new North American Podapolipoides (Acari: Podapolipidae), parasites of *Schistocerca piceifrons* (Walker) (Orthoptera: Acrididae) from Yucatan, Mexico. International Journal of Acarology 37:260–292. DOI: 10.1080/01647954.2011.564592.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth. London: International Trust for Zoological Nomenclature. pp. i–xxix + 1–306.

Mayoral JG. 2013. Notes on the genus *Beronium* (Acari, Eutrombidiinae) enlightened by new captures of *Beronium laemostenis* in Spain. Acarologia 53:425–427. DOI: 10.1051/acarologia/20122106.

Mayoral JG, Barranco P. 2005a. A new genus of the Eutrombidiinae Thor 1935 (Acari: Eutrombidiidae) parasitic on an endemic beetle from the south of Spain. Systematic Parasitology 62:111–115. DOI: 10.1007/s11230-005-5485-8.

Mayoral JG, Barranco P. 2005b. *Beronium laemostenis* sp. n. (Acari, Eutrombidiinae), a new larval mite on a troglobius beetle from Spain. Biologia - Section Zoology 60:125–128.

Pérez-Espinoza SA, Moreno Salas L. 2016. Parasitism of Ceroglossus buqueti (Coleoptera: Carabidae) by Hexathrombium mites (Acari: Microtrombidiidae): Body distribution, prevalence, intensity and attachment preferences in relation to body size and sex. International Journal of Acarology 42 (5):247–251. DOI:10.1080/01647954.2016.1178329.

Severin HC. 1944. The grasshopper mite *Eutrombidium trigonum* (Hermann) an important enemy of grasshoppers. South Dakota Experiment Station Technical Bulletin 3:1–36.

Southcott RV. 1986. Studies on the taxonomy and biology of the subfamily Trombidiinae (Acarina: Trombidiidae) with a critical revision of the genera. Australian Journal of Zoology, Suppl. Ser 123:1–116. DOI: 10.1071/AJZS123.

Southcott RV. 1993. Revision of the taxonomy of the larvae of the subfamily Eutrombidiinae (Acarina: Microtrombidiidae). Invertebrate Taxonomy 7:885–959. DOI: 10.1071/IT9930885.

Tetracha fulgida (Klug, 1834) in GBIF Secretariat. 2019. GBIF backbone taxonomy. Checklist dataset. DOI:10.15468/39omei. accessed via GBIF.org on 2019-12-03.

Vercammen-Grandjean PH. 1967. Revision of *Hoplothrombium quinquescutatum* Ewing, 1925 (Trombidiidae: Acarina). Opuscula Zoologica 96:1–7.

Welbourn WC. 1983. Potential use of trombidioid and erythraeoid mites as biological control agents of insects pests. In: Hoy MA, Cunningham GL, Knutson L, editors. Biological control of pests by mites. Berkeley: Agricultural Experiment Station, Division of Agriculture and Natural Resources, University of California. pp. 103–140. Special Publication 3304.

Wohltmann A, Gabryś G, Mąkol J. 2007. Acari: Terrestrial Parasitengona inhabiting transient biotopes. In: Gerecke R, editor. Süßwasserfauna von Mitteleuropa 7/2–1, Chelicerata, Araneae, Acari I. München: Spektrum Elsevier. pp. 158–240. [2006].

Zheng B. 1997. A new species of genus *Hexathrombium* Cooreman 1944 (Acari: Microtrombidiidae) from China. Entomologia Sinica 4:38–41.