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Revision of the New World *Ceratoculicoides* Wirth & Ratanaworabhan (Diptera, Ceratopogonidae, Ceratopogonini)

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Abstract. The New World species of the genus *Ceratoculicoides* Wirth & Ratanaworabhan are described, illustrated and keyed in both sexes. *Ceratoculicoides borkenti* sp. nov., *C. confusus* sp. nov., *C. grogani* sp. nov., *C. pacificus* sp. nov. and *C. propinquus* sp. nov. are described, with *C. confusus* being the first record of the genus from South America (Colombia). *Ceratoculicoides blantoni* is a junior synonym of *C. virginianus* and the identity of *C. longipennis* remains unclear as the male morphospecies associated in taxonomic literature with the female type series is not conspecific. A morphological phylogeny of all extant species in the genus is presented and characters discussed. The *moravicus* species group is recognized for a clade of species with the lateral margins of the aedeagus straight or concave.

Keywords. Biting midges, predaceous midges, phylogeny, Nearctic, Neotropical.

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Introduction

Ceratoculicoides Wirth & Ratanaworabhan, 1971 is a genus of small to mid-size (<1.8 mm wing length; Figs 1–2), poorly known predaceous midges that are collected only periodically, as adults and are entirely unknown as immatures. The genus is placed in the tribe Ceratopogonini, a paraphyletic grouping of genera (Borkent 2014) defined by the presence of palisade setae on the 1st tarsomere of the hind leg and a petiolate or obsolete M_{1+2} fork in the wing. Within the Ceratopogonini, *Ceratoculicoides* is phylogenetically related to several genera having 1–4 katepisternal setae including *Brachypogon* Kieffer, 1899 (Borkent 1995). Adults are most readily separated from all other Ceratopogonidae by a cluster of 2–3 setae on the posterior margin of the anterior anepisternum (Borkent 1992). *Ceratoculicoides* has been recorded from Europe (Havelka 1976, 1980; Knoz 1987; Delécolle & Schiegg 1998; Szadziewski & Knoz 2002), western Asia (Remm 1967), North America (Wirth 1951, 1952; Wirth & Ratanaworabhan 1971) and Central America (Huerta & Borkent 2005; Borkent *et al.* 2009), and here, for the first time, from northern South America. Life history and bionomic information is scant, with ecological studies collecting species in traps near streams (Havelka 1976, 1980) and decaying wood (Delécolle & Schiegg 1998).

Ceratoculicoides was proposed by Wirth & Ratanaworabhan (1971) to contain three species (*Helea longipennis* Wirth, 1952, *Ceratopogon gracilipes* Remm, 1967 and *Helea virginiana* Wirth, 1951) previously assigned by Wirth (1965) and Remm (1967) to *Nilohelea* Kieffer, 1921, a name now considered a synonym of *Brachypogon* (*Isohelea*). *Ceratoculicoides longipennis* was designated as type species of the genus, and *C. blantoni* Wirth & Ratanaworabhan, 1971 described as a new species in the same publication. Wirth & Ratanaworabhan (1971) diagnosed *Ceratoculicoides* by a combination of the small claws on the female hind leg, absence of wing cell r_1 and diminution of r_2, and the obliteration of the base of vein M_2. They also noted that the shape of the male aedeagus was distinctive with a "low basal arch and short anterolateral basal arms; broad main portion with slightly cleft apex and bearing small, dorsally bent, apicolateral teeth," although the male morphospecies they described as *C. longipennis* lacked the cleft apex. Borkent (1992) distinguished *Ceratoculicoides* by the presence of setae on the posterior margin of the anterior anepisternum, a synapomorphy of the genus (Fig. 3). Subsequent authors (Szadziewski *et al.* 1997; Borkent *et al.* 2009) have used this as a primary character to diagnose the genus.

Ceratoculicoides moravicus Knoz, 1987 was subsequently described from southern Moravia (Knoz 1987), and Wirth & Grogan (1988) transferred *Ceratopogon tontoeguri* Havelka, 1980 to the genus. Wirth & Grogan (1988) found *Ceratopogon gracilipes* Remm, 1967 to be a junior primary homonym of *Ceratopogon gracilipes* Winnertz, 1852 (now *Bezzia gracilipes* (Winnertz)) and proposed *Ceratoculicoides havelkai* Wirth & Grogan, 1988 as a replacement name. Gosseries (1989) subsequently noted this homonymy as well, and unnecessarily proposed *Ceratoculicoides remmi* Gosseries, 1989 as a replacement name. Szadziewski (1988) described the only known fossil member of the genus, *Ceratoculicoides danicus* Szadziewski, 1988, from Baltic amber.

Delécolle & Schiegg (1998) recognized *C. remmi* as a junior objective synonym of *C. havelkai* in their revision of the Palaearctic fauna, and also considered *C. moravicus* as a junior subjective synonym of *C. havelkai*, although *C. moravicus* was the older name. Szadzewski & Knoz (2002) corrected that oversight, listing *C. gracilipes*, *C. havelkai* and *C. remmi* as synonyms of *C. moravicus*. The description of *Ceratoculicoides aliciae* Huerta & Borkent, 2005 expanded the range of the genus into the Neotropical region, and they noted an undescribed species known only as females from Costa Rica.

This study is based on the examination of new material of *Ceratoculicoides* from the Nearctic and Neotropical regions, which revealed the presence of five undescribed species named here and four additional morphospecies given provisional designations. *Ceratoculicoides blantoni* is recognized as a synonym of *C. virginianus*, and progress made in clarifying the application of the name *C. longipennis*. Additionally, a morphological character set was recorded and analyzed to produce a species level phylogeny within the genus.

Material and methods

Specimens were procured on loan from the Canadian National Collection of Insects, Arthropods and Nematodes (CNCI), Florida State Collection of Arthropods (FSCA), Smithsonian National Museum of Natural History (USNM), Art Borkent (to be deposited at CNCI upon completion of this study) and my own personal collection (AFPC). All specimens examined were mounted on slides, unless otherwise noted. As male material of *C. aliciae* was not available for this study, only a diagnosis and reference illustrations are given. Material was examined using Olympus CH and Leica DM1000 compound microscopes, with habitus photographs taken using a Leica S8APO stereo microscope. Photomicrographs were taken using an Amscope DM1000 camera and Amscope 3.7.7303 software, which were also used for calibrated measurements. Focus stacked images were compiled using CombineZP (Hadley 2008). Illustrations were created with Inkscape ver. 1.1.

Table 1. Morphological character matrix. Morphological character set: **1**. Setae on posterior margin of anterior anepisternum: 0 = absent; 1 = present (Fig. 3). **2**. Dorsocentral punctuations on scutum of female: 0 = absent; 1 = present. **3**. Sternite 9 of female: 0 = pointed or rounded; 1 = C-shaped (Figs 11–12). **4**. Number of major spermathecae: 0 = 2; 1 = 1. **5**. Length of largest spermatheca: 0 = < 80 μm; 1 > 80 μm. **6**. Lateral margins of aedeagus: 0 = convex (Fig. 8c, f, i); 1 = straight or concave (Figs 9f, i, 10h, k). **7**. Posterior margin of aedeagus: 0 = convex (Fig. 8c, f, i); 1 = straight or concave (Figs 9f, i, 10h, k). **8**. Posteromedial hyaline incision of aedeagus: 0 = absent (Fig. 8c, f); 1 = present (Figs 8i, 9f, i). **9**. Posterolateral point of aedeagus: 0 = absent; 1 = dorsally directed (at base) (Fig. 8c, f); 2 = directed laterally (at base) (Figs 9f, i, 10h, k). **10**. Apex of posterolateral point of aedeagus: 0 = spiniform (Fig. 9i); 1 = rounded (Fig. 10h, k). **11**. Apical point of aedeagus: 0 = absent (Fig. 8c, f); 1 = separate from posterolateral point (if present) (Fig 8i); 2 = adjacent to or contiguous with posterolateral point (Figs 9c, f, i, 10h, k). **12**. Accessory point between apical and posterolateral points: 0 = absent (Figs 9f, i, 10k); 1 = present (Fig. 10c, h).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Sinhalohelea gansi Grogan & Borkent, 1992	0	0	0	0	0	0	0	0	0	–	0	–
Brachypogon canadensis Downes, 1976	0	0	0	1	0	0	0	0	0	–	0	–
Brachypogon sp. L	0	0	0	0	0	1	1	1	0	–	1	–
Ceratoculicoides alicae Huerta & Borkent, 2005	1	1	1	0	0	1	1	1	2	1	2	0
C. borkenti sp. nov.	1	1	1	0	0	1	1	1	2	0	2	0
C. confusus sp. nov.	1	1	1	0	1	0	0	0	1	0	0	–
C. grogani sp. nov..	1	1	1	0	0	1	1	1	2	0	2	0
Ceratoculicoides sp. M1	1	?	?	?	?	1	1	1	2	1	2	1
C. moravicus Knoz, 1987	1	1	1	1	1	1	1	1	2	1	2	1
C. pacificus sp. nov.	1	1	1	0	1	0	0	1	1	0	1	0
C. propinquus sp. nov.	1	?	?	?	?	1	1	1	2	1	2	0
C. tontoeguri Havelka, 1980	1	1	1	0	1	0	1	1	2	0	2	0
C. virginianus (Wirth, 1951)	1	1	1	0	0	0	1	0	1	0	2	0

Terminology follows Borkent (2017) and Cumming & Wood (2017). Species diagnoses are given as the minimum combination of characters to identify a given species from other species in *Ceratoculicoides*. Measurements are in μm unless otherwise noted. Measurements used (arranged alphabetically): aedeagus ratio: length from apex of basal arch to apex of aedeagus (excluding spiniform points)/width of midpoint between basal arch and apex of aedeagus; antennal ratio (AR): flagellomeres 11–13/1–10 (males), 9–13/1–8 (females); costal ratio: costa length/wing length as measured from the arculus; flagellum/head ratio (FR): antennal flagellum length divided by head width; gonocoxite ratio (GCR): gonocoxite length/width (excluding gonocoxal apodeme); gonostylus/gonocoxite ratio (GSR): length of gonostylus/length of gonocoxite; head width: widest point along transverse axis; spermatheca length: base of neck to furthest point of body; spermatheca neck: length from apex of neck to point where it meets the contour of the body; spermatheca/neck ratio (SR): spermatheca neck length/spermatheca length; spermatheca width: widest point on axis perpendicular to neck; wing length: length from termination of axillary sclerites to apex of wing; wing width: widest point perpendicular to leading edge; wing ratio: wing length/width. Measurements based on multiple specimens are given as minimum–maximum (median); when flagellomeres are fused the sclerotized "neck" between two flagellomeres is measured as part of the proximal article; the apodeme of the 1st flagellomere which inserts in the pedicel is not

measured, nor is the non-sclerotized break between flagellomeres. Female descriptions only include characters differing from the male; only the largest spermatheca was measured per specimen; the term major spermathecae is used to differentiate the large, round first and second spermathecae from the rudimentary third spermatheca often present. For bilaterally symmetrical structures on the midline only one half is described and/or enumerated. No taxonomically relevant chaetotaxy except for the dorsocentral punctations of the scutum was found at the species level, so these characters are omitted from the descriptions and illustrations.

For the phylogenetic analysis morphological characters were directly scored from specimens, except *Sinhalohelea gansi* Grogan & Borkent, 1992, *C. aliciae* and *C. tontoeguri*, which were scored from the original descriptions and Delécolle & Schiegg (1998). *Sinhalohelea gansi*, *Brachypogon* (*Brachypogon*) *canadensis* Downes, 1976 and *Brachypogon* (*Isohelea*) sp. L (sensu W.L. Grogan, specimens in FSCA) were used as outgroups. Inapplicable character states were scored as "-" and missing data as "?;" none of the characters were weighted. The resulting dataset comprised 11 taxa (three outgroup, eight ingroup) and 12 characters (Table 1). Mesquite ver. 3.61 (Maddison & Maddison 2019) was used to build the character matrix and interpret character state distributions and polarity, with TNT 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) used for a Maximum Parsimony analysis of the dataset via an Implicit Enumeration search (since the number of taxa is small enough to sample the entire treespace), and the Bremer Support function to find the branch support on the tree. Bootstrap values were also calculated but are not included in the results, as none exceeded the threshold value of 50. The tree figure was initially generated using iToL (Letunic & Bork 2019) and finalized with Inkscape.

Results

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Family Ceratopogonidae Newman, 1834
Subfamily Ceratopogoninae Newman, 1834
Tribe Ceratopogonini Newman, 1834

Ceratoculicoides Wirth & Ratanaworabhan, 1971
Figs 1–12

Ceratoculicoides Wirth & Ratanaworabhan, 1971: 170.

Ceratoculicoides – Downes & Wirth 1981: 408 (included in genus key). — Knoz 1987: 391 (diagnosis), 388 (species key). — Wirth & Grogan 1988: 6 (included in genus key), 39 (diagnosis). — Borkent 1992: 434 (included in genus key). — Borkent & Wirth 1997: 95 (in catalog). — Huerta & Borkent 2005: 114 (catalog). — Borkent *et al.* 2009: 413 (included in genus key). — Borkent & Dominiak 2020: 157 (in catalog).

Type species

Helea longipennis Wirth, 1952: 170 (by original designation).

Diagnosis (adult)

Anepisternum with 1–3 setae along posterior margin, katepisternum with 2–4 setae. Tarsomere 1 of hind leg with palisade setae. Wing cells r_1 and r_2 reduced, M_2 base obsolete.

Description

Male

Head. Cranium brown. Antenna brown with 13 flagellomeres, 7–11 always fused, fusion sometimes including flagellomeres 5 and 6 as well; 2–3 sensilla coeloconica on 1, flagellomeres 1–10 with plume,

11–12 with ring of laterally directed trichoid sensilla at base, 13 with apical trichoid sensillum, AR 0.65–1.02, FR 1.49–1.92. Eyes separated medially by diameter of 3–5 ommatidia, ommatrichia present. Palpus brown, with 5 segments, 3rd with sensory pit.

Thorax. Scutum, scutellum and pleural sclerites dark brown without distinct coloration patterns; scutum without anteromedial tubercle, humeral pits poorly developed, often with punctations present among dorsocentrals. Anepisternum with 1–3 setae along posterior margin, katepisternum with 2–4 setae.

Wing. Cells r_1 and r_2 reduced, M_2 base obsolete. Membrane with microtrichia, macrotrichia present only on C and R; membrane unpatterned, without macrotrichia.

Legs. Femora, tibiae without spines; spur formula 1-0-1, hindleg spur pectinate. Hind 1st tarsomere with single row of palisade setae; all tarsal claws equal-sized, without accessory teeth, straight, apex minutely bifid.

Pregenital abdomen. Brown, without distinct coloration patterns, margins roughly parallel to genitalia.

Genitalia. Epandrium with apicolateral processes present, cerci and proctiger near posterior margin of epandrium directed ventrally. Gonocoxite cylindrical; gonocoxal apodeme quadrate anteriorly, triangular posteriorly; gonostylus simple, subequal in length to gonocoxite, weakly curved at tip. Sternite 9 (hypandrium) slightly tapering anteriorly, length/width ratio 0.33, with medial emargination. Parameres

Fig. 1. *Ceratoculicoides pacificus* sp. nov., male habitus (CNCI). Scale bar = 100 μm.

separate or weakly fused at base; articulating with anterior portion of gonocoxal apodeme, apical arms of paramere stylate, directed posteriorly at distinct angle from base, midpoint arched dorsally in lateral view, apex of paramere ventrally directed, extending to apex of aedeagus or beyond. Aedeagus heavily sclerotized, with or without apical hyaline incision medially, with distinct basal arms articulated on anterior portion of gonocoxal apodeme, posterolateral point present, of variable form.

Female

Head. All flagellomeres separate, without plume, AR 1.08–1.33, FR 1.37–1.83. Mandible with 8 teeth.

Thorax. Dorsocentral portion of scutum with numerous punctations.

Wing. Membrane with scattered macrotrichia along apical margin.

Legs. Fore-, midleg tarsal claws longer than those of hindleg, equal or slightly unequally sized, gently curving along length, apex with simple point.

Pregenital abdomen. Margins convex, widest at approximately ⅓ length in specimens fully laden with eggs, posteriorly tapering to rounded apex.

Fig. 2. *Ceratoculicoides pacificus* sp. nov. (CNCI), female habitus. Scale bar = 100 μm.

Genitalia. Tergite 9 simple, bandlike. Sternite 8 simple, undivided. Sternite 9 narrow at base, apex crescent-shaped. 1–2 major spermathecae and a very small third spermatheca usually present. Spermathecal necks weakly curved, spermathecal neck ratio 0.14–0.32.

Immature stages

Currently unknown.

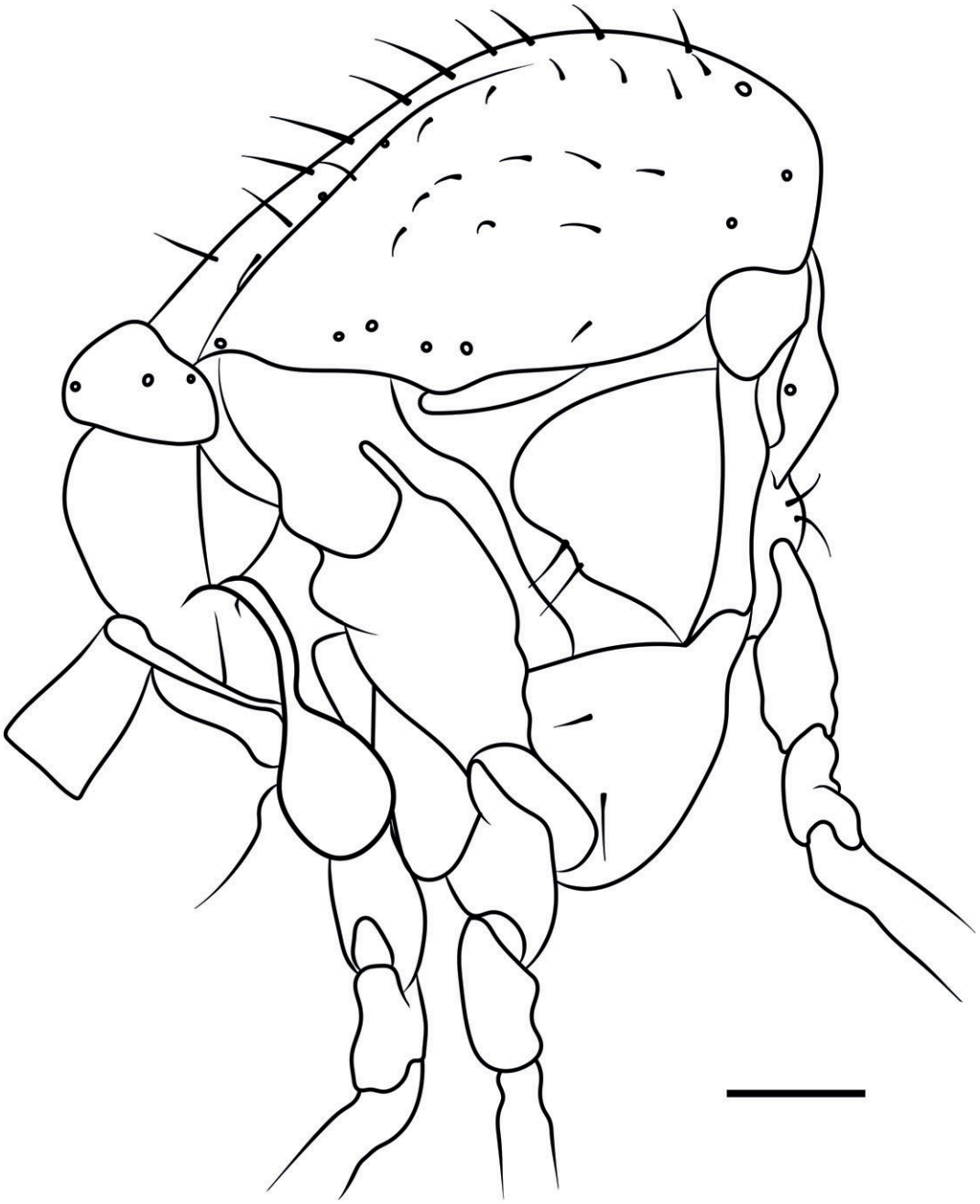

Fig. 3. *Ceratoculicoides pacificus* sp. nov. (CNCI), male thorax. Scale bar = 100 μm.

Key to adult male New World Ceratoculicoides

The male lifestage of *Ceratoculicoides longipennis* from California is currently unknown. A poorly preserved male specimen from California that may be conspecific with *C. longipennis* is included as *C*. sp. M1 in the key. The distribution of each species is noted in brackets.

1. Apex of paramere broadly rounded, minimally tapering to apex, minute apical point laterally displaced (Fig. 9b) [eastern North America (Canada and USA)] ..... ***C. virginianus*** (Wirth, 1951)
– Apex of paramere acute, paramere evenly tapers to apical point that is not laterally displaced (Fig. 9e, h) 2

2. Lateral margin of aedeagus evenly convex, without constriction (Fig. 8c, f, i) 3
– Lateral margin of aedeagus straight (Fig. 10c), apically constricted (Figs 9c, 10e, h) or concave (Fig. 9f, i) 4

3. Medial apex of aedeagus with hyaline incision, length of dorsolateral spines >0.5 width of apex of aedeagus (Fig. 8i) [Pacific Northwest (Canada and USA)] ..... ***C. pacificus*** sp. nov.
– Medial apex of aedeagus uniformly sclerotized, without hyaline medial incision, length of dorsolateral spines >0.25 width of apex of aedeagus (Fig. 8c, f) [eastern North America (Canada and USA) and Colombia].. .....***C. confusus*** sp. nov.

4. Aedeagus with posteromedial hyaline incision extending nearly to basal arch, anterior apex broad (Fig. 9f) [Southwestern United States, Rocky Mountains (USA), Vancouver Island (Canada)] .... ***C. borkenti*** sp. nov.
– Aedeagus hyaline incision tapering or obscure anteriorly (Figs 9i, 10h, k) 5

5. Aedeagus lateral margins narrowed apically, posterior margin of aedeagus with distinct notch (Fig. 10e) [Jalisco (Mexico)] ..... ***C. aliciae*** Huerta & Borkent, 2005
– Aedeagus lateral margins straight, posterior margin an even arc, without notch (Figs 9i, 10c, k) [Pacific Northwest and California (Canada and USA)] 6

6. Posterolateral point of aedeagus an acutely pointed spine, much longer than basal width, apex directed laterally (Fig. 9i) [Oregon and California (USA)] ..... ***C. grogani*** sp. nov.
– Posterolateral point of aedeagus rounded, length subequal to basal width, directed slightly anteriorly (Fig. 10c, k) 7

7. Accessory points present between apical and posterolateral points of aedeagus (Fig. 10c), wing length >1.1 mm [California (USA)] ..... *C.* sp. M1
– Accessory points absent between apical and posterolateral points of aedeagus (Fig. 10k), wing length <1.1 mm [British Columbia (Canada) and California (USA)] ..... ***C. propinquus*** sp. nov.

Key to the adult female New World Ceratoculicoides

Ceratoculicoides longipennis from California, known only as a female, is not included in the following key. Three female morphotypes are included but not formally named (see taxonomic discussions below). Individual species distributions are noted in brackets.

1. Medial margin of female genital sclerotization on sternite 9 almost straight (Fig. 11e) [Oregon and California (USA)] ..... ***C. grogani*** sp. nov.
– Median margin of female genital sclerotization on sternite 9 strongly concave, arched (Figs 11a–d, f, 12a–f) 2

2. Length of largest spermatheca >80 µm 3
– Length of largest spermatheca <80 µm 4

3. Wing length <1.5 mm [eastern North America (Canada and USA)] ..... ***C. confusus*** sp. nov.
– Wing length >1.5 mm [Pacific Northwest (Canada and USA)] ..... ***C. pacifica*** sp. nov.

4. Length of largest spermatheca >70 µm 5
– Length of largest spermatheca <70 µm 6

5. Posterior branch of 9th sternite tapering, apex acutely pointed (Fig. 11a) [Jalisco (Mexico)] ..... ***C. aliciae*** Huerta & Borkent, 2005
– Posterior branch of 9th sternite not tapering, apex obtusely rounded (Fig. 12e) [Colombia] ..... *C.* sp. F2

6. Flagellum ratio (FR) <1.5 (Fig. 7c) [Southwestern United States, Rocky Mountains (USA), Vancouver Island (Canada)] ..... ***C. borkenti*** sp. nov.
– Flagellum ratio (FR) >1.5 (Figs 6a–d, 7d–e) 7

7. Anterior branch of 9th sternite tapering from base, acutely spiniform (Fig. 12f) [Costa Rica] ..... *C.* sp. F3
– Anterior branch of 9th sternite tapering only in apical half (Fig. 12c–d) ..... ***C. virginianus*** [eastern North America (Canada and USA), *C.* sp. F1 (Colombia)]

Ceratoculicoides moravicus species group

Figs 5, 7, 9d–i, 10–11

Diagnosis (male)

Those species of *Ceratoculicoides* with their aedeagus lateral margins straight or concave (Figs 9f, i, 10c, e, h, k).

Description (male)

Aedeagus lateral margins straight or concave, posterior margin straight or concave. Hyaline posteromedial incision of aedeagus present. Posterolateral points of aedeagus directed laterally, adjacent or contiguous with apical points.

Remarks

The *C. moravicus* group is proposed for *C. moravicus*, *C. aliciae*, *C. borkenti* sp. nov., *C. grogani* sp. nov., *C. propinquus* sp. nov. and *C.* sp. M1. All of these species share similar aedeagal characters, most notably the synapomorphy of straight or concave lateral margins of the aedeagus. There are no female characters that can be used to diagnose this group.

Ceratoculicoides aliciae Huerta & Borkent, 2005

Figs 7a–b, 10d–e, 11a

Ceratoculicoides aliciae Huerta & Borkent, 2005: 112, figs 1–21. (in catalog).

Ceratoculicoides aliciae – Borkent & Dominiak 2020: 157 (in catalog).

Diagnosis

Male

Ceratoculicoides aliciae can be separated from congeners by the following combination of characters: femora and tibiae yellow; apices of parameres acute, tapering; aedeagus lateral margins parallel basally, tapering apically, posterior margin with acute medial notch, apical and posterolateral point adjacent, posterolateral point rounded (Fig. 10e).

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.48; femora and tibiae yellow; wing length ~ 1.1 mm; 2 major spermathecae, largest 70–76; medial margin of 9th sternite deeply concave.

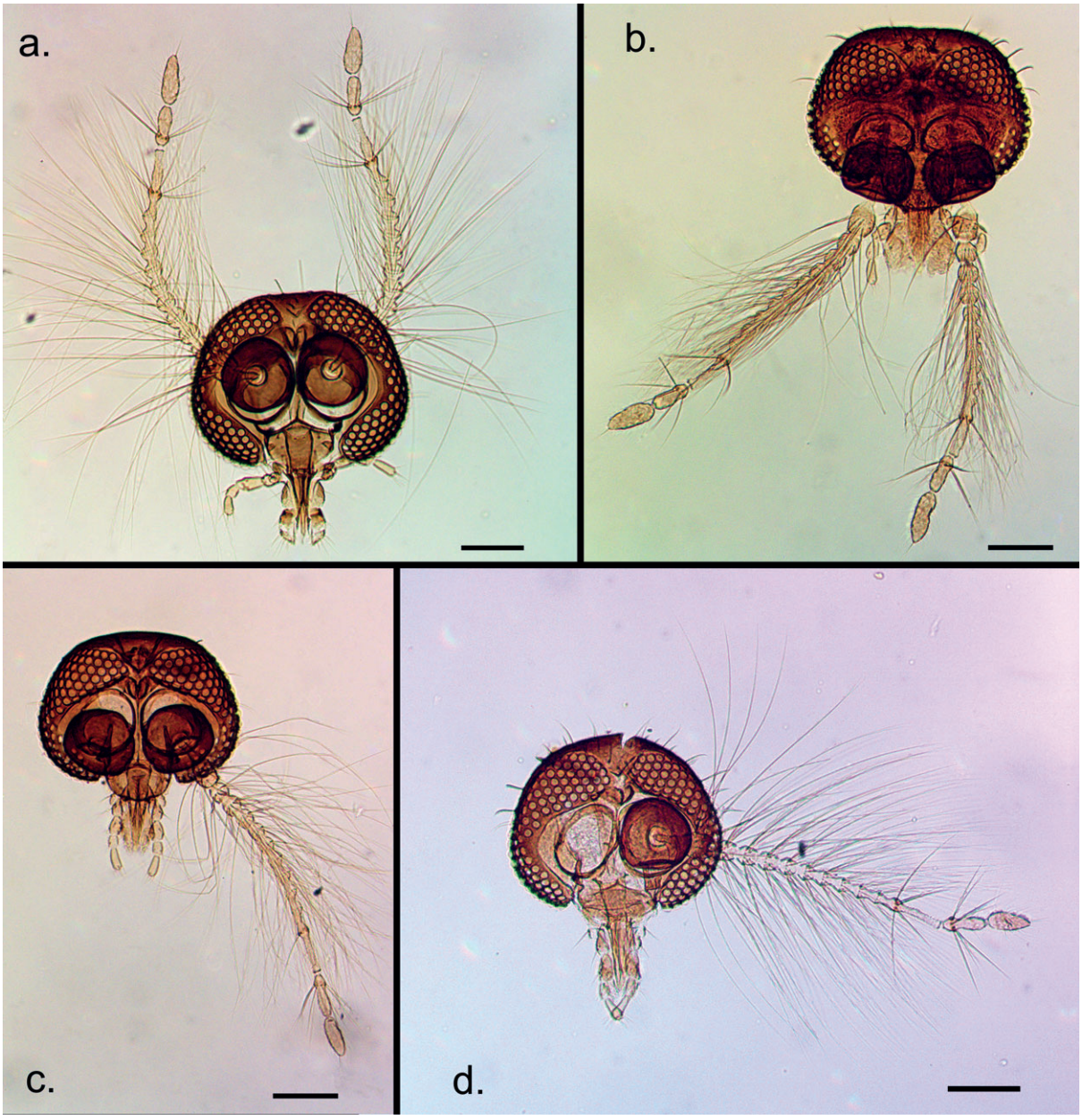

Fig. 4. Male heads I. **a**. *Ceratoculicoides confusus* sp. nov. **b**. *C. pacificus* sp. nov. **c**. *C. confusus* (Colombia). **d**. *C. virginianus* (Wirth, 1951). Scale bars = 100 μm.

Type material

Holotype

MEXICO • ♂; Jalisco, Biology Station Chamela; 6–11 Jul. 1992; A. Rodriguez leg.; Malaise trap; InDRE. Not examined in this study.

Material examined

Paratypes

MEXICO • 2 ♀♀; same collection data as for holotype; CNCI CAIMCrt/lam-01103, CAIMCrt/lam-01109.

Description (female)

Measurements (n = 2). Head width 280–332; flagellomeres (n = 1) 32, 20, 24, 27, 31, 31, 32, 35, 50, 47, 50, 52, 61; AR (n = 1) 1.12; FR (n = 1) 1.48; wing length 1.0–1.1 mm; wing width 0.42–0.43 mm; costal ratio (n = 1) 0.58; spermathecal length 71–76; spermathecal width 53–59; spermathecal neck 8–10; spermatheca/neck ratio 0.16.

Thorax. Legs with femora and tibiae yellow.

Genitalia (Fig. 11a). 9th sternite anterior branch blunt and poorly sclerotized medially, apices nearly touching; posterior branch curving towards tip, tapering near apex to acutely pointed tip. 2 major spermathecae.

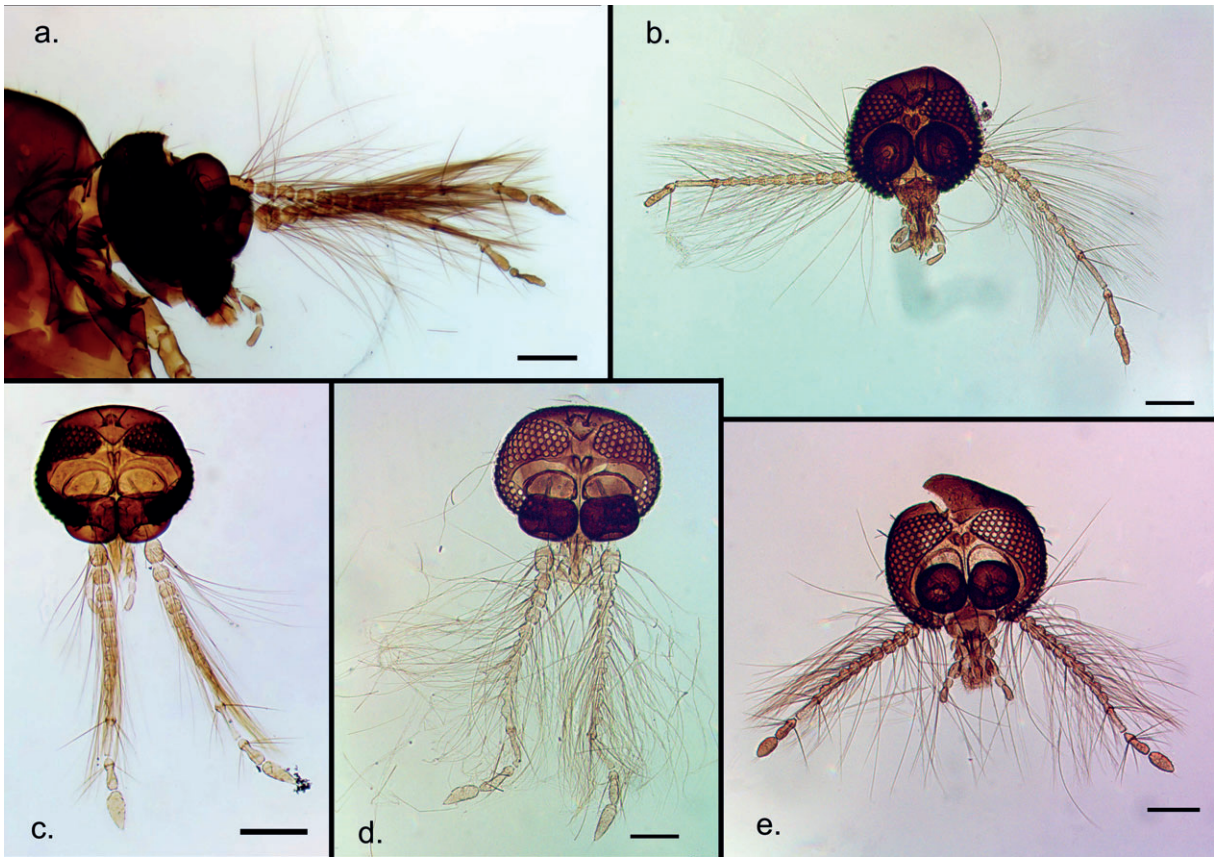

Fig. 5. Male heads II. *Ceratoculicoides moravicus* group. **a**. *C.* sp. M1. **b**. *C. moravicus* Knoz, 1987. **c**. *C. propinquus* sp. nov. **d**. *C. grogani* sp. nov. **e**. *C. borkenti* sp. nov. Scale bars = 100 μm.

Distribution

Jalisco (Mexico) (Fig. 13).

Remarks

As I did not examine the holotype, I cannot provide a full description of this species, but I did have the opportunity to examine the two female paratypes. Based on the description and illustrations of the male in Huerta & Borkent (2005), this species belongs in the *C. moravicus* group, similar to *C.* sp. M1, *C. moravicus* and *C. propinquus* sp. nov., based on the presence of accessory spines between the apical and posterolateral points of the aedeagus. Males of *C. aliciae* (Fig. 10e) can be recognized by the straight margins of the aedeagus narrowed conspicuously beyond their midpoint, the posterior margin with a distinct acute notch, and the apical and posterolateral points being adjacent. The females can be recognized by the largest spermatheca being 70–76 µm, a feature

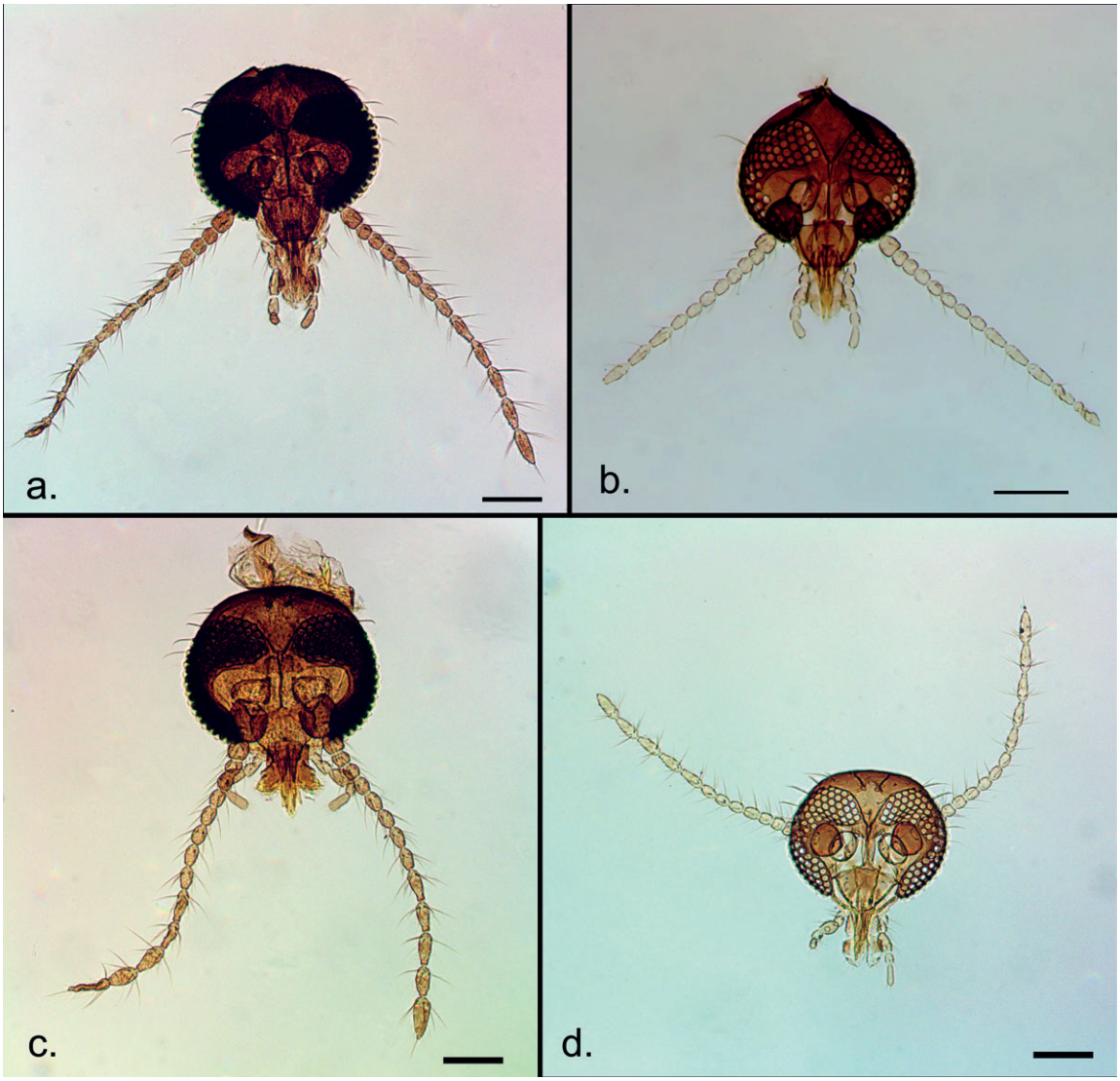

Fig. 6. Female heads I. **a**. *Ceratoculicoides confusus* sp. nov. **b**. *Ceratoculicoides* sp. F2 (Colombia). **c**. *C. pacificus* sp. nov. **d**. *C. virginianus* (Wirth, 1951). Scale bars = 100 µm.

found only in *C. moravicus* and an undescribed Colombian morphospecies (*C.* F2, Figs 7b, 12d; see taxonomic notes on *C. confusus*). Females of *C. aliciae* can be distinguished by the posterior branch of the 9th sternite tapering to an acute point, unlike the broadly rounded posterior branch of *C.* sp. F2. Both species are distinguished from *C. moravicus* by the presence of two major spermathecae.

Ceratoculicoides borkenti sp. nov.
urn:lsid:zoobank.org:act:545F2DF7-08BE-4ACD-B8D8-B18BC4F57A7D
Figs 5e, 7c, 9d–f, 11b

Diagnosis

Male

Ceratoculicoides borkenti sp. nov. can be separated from congeners by the following combination of characters: femora and tibiae brown; apices of parameres acute, tapering distally; aedeagus lateral margins an evenly concave arc, nearly entire medial portion of aedeagus hyaline, expanding anteriorly (Fig. 9f).

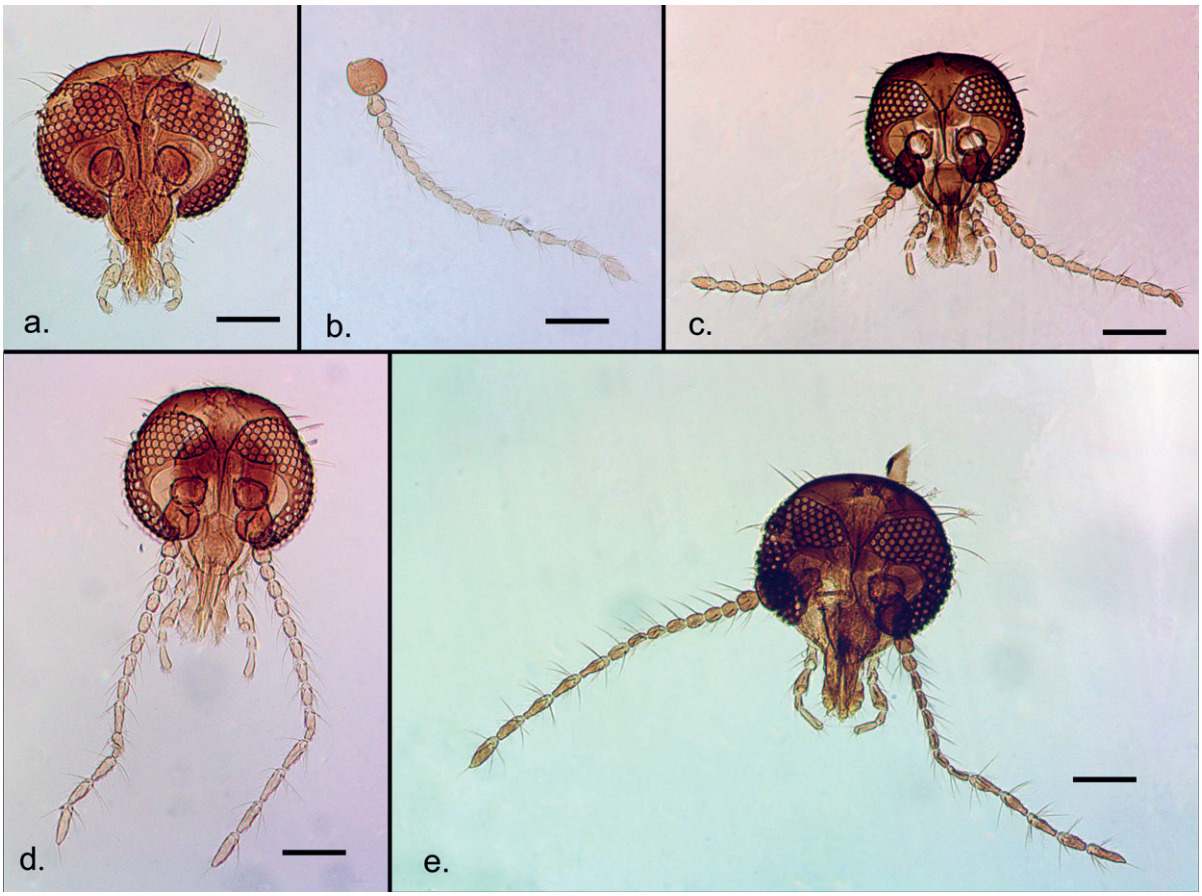

Fig. 7. Female heads II. *Ceratoculicoides moravicus* group. **a**. *C. aliciae* Huerta & Borkent, 2005. **b**. *C. aliciae* antenna. **c**. *C. borkenti* sp. nov. **d**. *C. grogani* sp. nov. **e**. *C. moravicus* Knoz, 1987. Scale bars = 100 μm.

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.41–1.47; femora and tibiae brown, wing length 1–1.2 mm; 2 major spermathecae, largest 52–67; medial margin of 9th sternite deeply concave.

Etymology

This species is named in honor of Art Borkent for encouraging my study of Ceratopogonidae, including suggesting this project after I collected a specimen of this species.

Material examined

Holotype

USA • ♂; Arizona, Santa Cruz Co., 24 km W of Nogales; 1 May 1987; A. Borkent leg.; CNCI.

Paratypes

USA • 1 ♂, 3 ♀♀; same collection data as for holotype; CNCI.

Other material

CANADA • 1 ♂; British Columbia, 25 km W of Lake Cowichan; 8 Jul. 1991; A. Borkent leg.; CNCI.

USA • 3 ♂♂; Arizona, Santa Cruz Co., 11 km SW of Patagonia; 29 Apr. 1987; A. Borkent leg.; CNCI • 2 ♂♂; same collection data as for preceding; Portal; 23 Apr. 1987; CNCI • 1 ♀; same collection data as for preceding; Yavapai Co., 19 km S of Sedona; 8 May 1987; CNCI • 1 ♂; California, Riverside Co., Philip L. Boyd Deep Canyon Desert Research Center, Horsethief Creek; 5 Apr. 1970; L. Lapre leg.; USNM • 2 ♂♂; same collection data as for preceding; Thousand Palms; 3 Apr. 1955; W.R. Mason leg.; USNM • 1 ♂; Idaho, Idaho Co., Clearwater National Forest, Imnamatnoon Creek; 46.5149° N, 114.7635° W; 15 Jul. 2017; A. Fasbender leg.; AFPC • 1 ♂; Montana, Missoula Co., Lolo National Forest, East Fork Lolo Creek at US 12; 46.7125° N, 114.5324° W; 26 Jun. 2021; A. Fasbender leg.; AFPC.

Description

Male

Measurements (n = 5). Head width (n = 3) 293–305(305); flagellomeres 34–48(45), 22–28(26), 23–29(25), 22–25(24), 20–27(24), 24–27(25), 25–27(25), 23–30(27), 21–29(25), 21–32(25), 65–86(68), 53–64(56), 55–65(58); AR 0.65–0.76(0.69); FR (n = 1) 1.49; wing length 0.95–1.0(0.97) mm; wing width 0.35 mm; costal ratio (n = 1) 0.50; GCR 2.13–2.62(2.42); GSR 0.82–0.89(0.86); aedeagus ratio (n = 3) 3.33–3.67(3.65).

Thorax. Dorsocentral punctations inconspicuous, present only at posteriormost portion of dorsocentral setae near scutellum, may be absent in some specimens. Legs with femora and tibiae brown.

Genitalia (Fig. 9d–f). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins concave, smoothly rounded, apical point posterolaterally directed, triangular with adjacent lateral obtuse spur-like posterolateral point without accessory spines, posterior margin emarginate, hyaline, hyaline medial incision extensive, margins parallel to lateral margins and basal arch.

Female

Measurements (n = 4). Head width (n = 3) 253–278; flagellomeres (n = 3) 26–28(27), 15–17(15), 18–20(20), 20–28(21), 21–25(24), 17–24(24), 24–27(25), 25–31(30), 39–41(40, 35–43(42), 40–46(40), 30–40(38), 41–50(43); AR 1.08–1.15; FR 1.41–1.47; wing length 0.97–1.19(1.13) mm; wing width

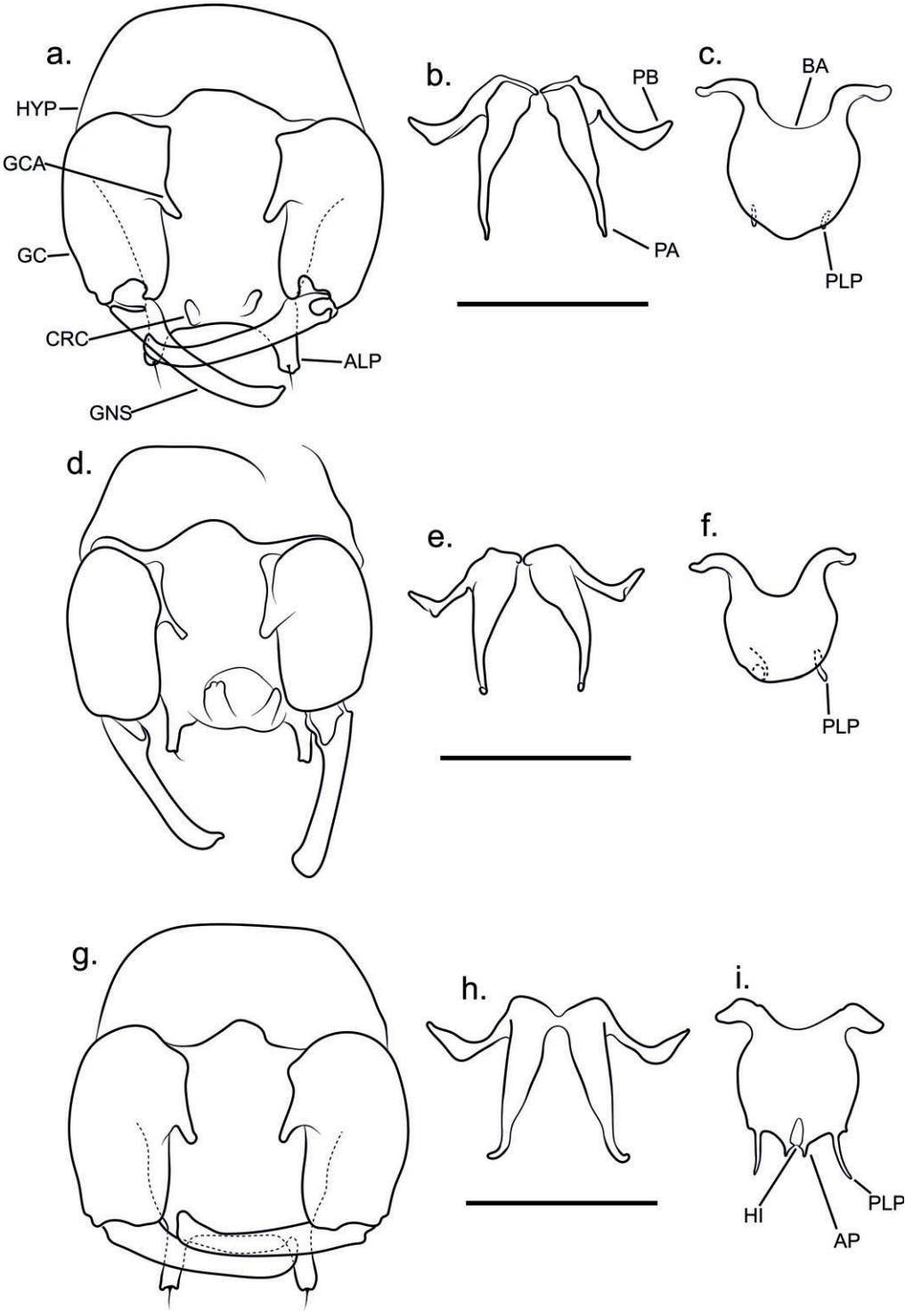

Fig. 8. Male genitalia I. *Ceratoculicoides confusus* sp. nov.: **a**. Genitalia, aedeagus and parameres removed. **b**. Parameres. **c**. Aedeagus. *C. confusus* (Colombia): **d**. Genitalia, aedeagus and parameres removed. **e**. Parameres. **f**. Aedeagus. *C. pacificus* sp. nov: **g**. Genitalia, aedeagus and parameres removed. **h**. Parameres. **i**. Aedeagus. Abbreviations: ALP = apicolateral point of epandrium; AP = apical point of aedeagus; BA = basal arch of aedeagus; CRC = cercus; GC = gonocoxite; GCA = gonocoxal apodeme; GNS = gonostylus; HI = hyaline incision of aedeagus; HYP = hypandrium; PA = paramere apex; PB = paramere base; PLP = posterolateral point of aedeagus. Scale bars = 100 μm.

0.40–0.52(0.45) mm; costal ratio (n = 1) 0.55; spermathecal length 52–67(61); spermathecal width 37–49(43); spermathecal neck 9–16(14); spermatheca/neck ratio 0.22.

Thorax. Legs with femora and tibiae brown.

Genitalia (Fig. 11b). 9th sternite anterior branch acutely pointed, apices of each half touching medially or not; posterior branch evenly curving towards apex, spiniform, tip acute to rounded. 2 major spermathecae.

Distribution

British Columbia (Canada); Arizona, California, Idaho, Montana (USA) (Fig. 13).

Remarks

Ceratoculicoides borkenti sp. nov. is one of the most distinctive species of *Ceratoculicoides* in the adult male life stage. As member of the *C. moravicus* group, the lateral margins of the aedeagus are heavily sclerotized, deeply concave, and taper in a smooth arc to a narrow apex (Fig. 9f). The median portion of the aedeagus is so hyaline as to be nearly transparent, and unlike any other *Ceratoculicoides* the hyaline incision expands above the basal arch subtrapezoidally, leaving only the lateral and anterior margins of the aedeagus sclerotized.

The females of *C. borkenti* sp. nov. (Fig. 11b) fall into a group of several species with the length of the largest spermathecae <70 μm. Of the described species, it can be differentiated from *C. grogani* sp. nov. by the medial margin of the 9th sternite being deeply concave and rounded (vs nearly straight and sinuous, Fig. 11e) and *C. virginianus* (Fig. 12c) by the 9th sternite's acute or triangular anterior branch (vs rounded or truncate) and evenly curved posteromedially directed spiniform posterior branch (base of branch directed posteriorly, curving medially in apical half in *C. virginianus*, usually tapering only in apical portion). However, there are a number of unassociated female specimens which display a similar morphology, including a species from Colombia (*C.* sp. F1, Fig. 12c) and another from Costa Rica (*C.* sp. F3, Fig. 12e). The Costa Rican *C.* sp F3 differs in having the base of the posterior branch directed posteriorly, vs evenly curving along the whole length in *C. borkenti*, but *C.* sp. F1 from Colombia cannot be reliably differentiated by the 9th sternite. *C. borkenti* has a lower flagellum ratio (FR <1.5) than either of these provisional species. As there is only a limited sample of reliably associated females, and there are two male morphospecies without a female association sharing the range of *C. borkenti* (*C. propinquus* sp. nov. and *C.* sp. M1), the characters cited above may prove non-diagnostic upon examination of a broader range of material.

Ceratoculicoides grogani sp. nov.
urn:lsid:zoobank.org:act:D295FBE0-C019-4CA5-A608-C4EA7525D529
Figs 5d, 7d, 9g–i, 11e

Diagnosis

Male

Ceratoculicoides grogani sp. nov. can be separated from congeners by the following combination of characters: femora and tibiae yellow or lightly infuscate; apices of parameres acute, tapering distally; aedeagus lateral margins straight, posterolateral point an acute spine directed laterally (Fig. 9i).

Female

Only species of *Ceratoculicoides* with the following combination of characters: hind femur infuscate, other femora and tibiae brown, wing length ~1.4 mm; 2 spermathecae, largest 60; medial margin of 9th sternite weakly concave, sinuous.

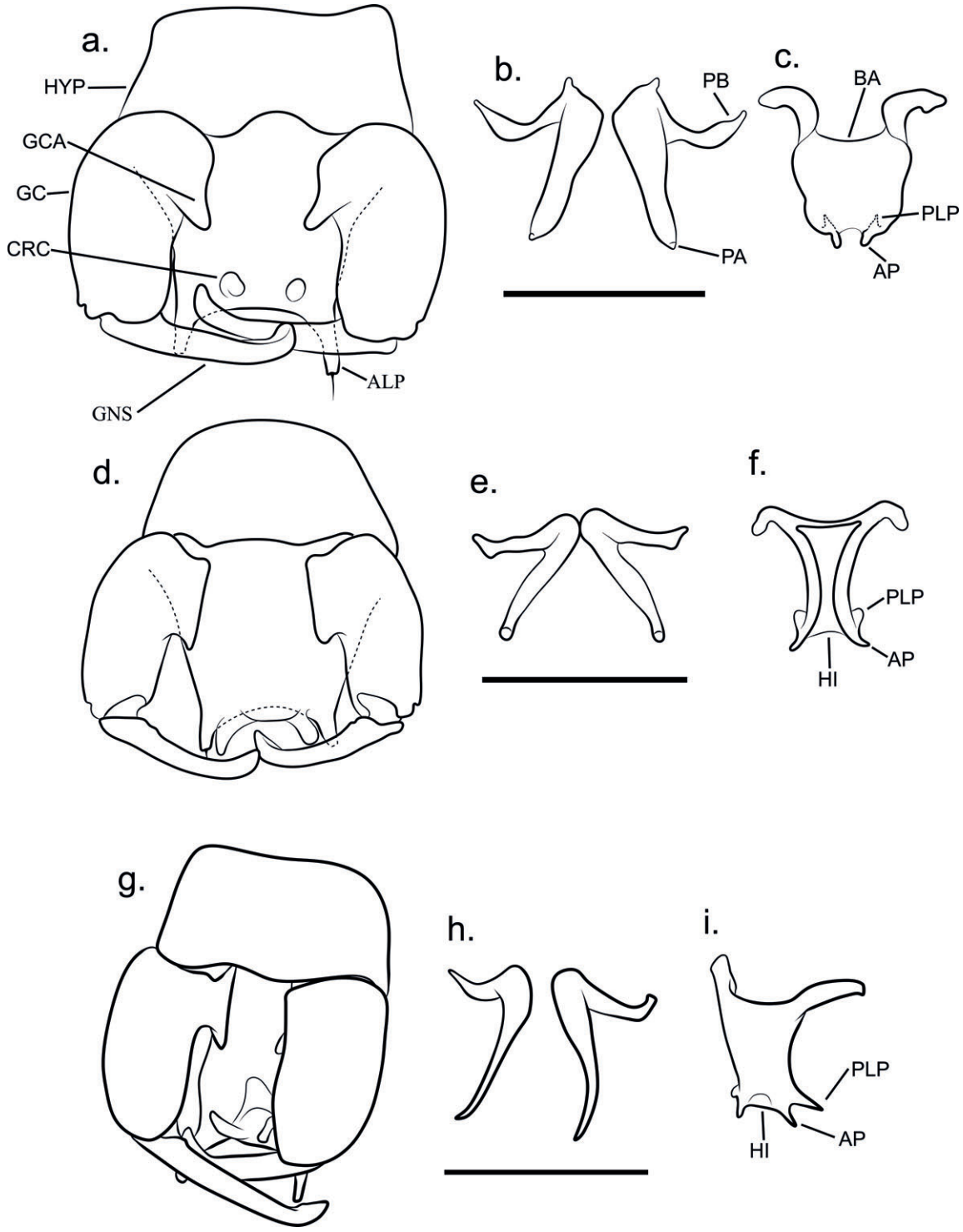

Fig. 9. Male genitalia II. *Ceratoculicoides virginianus* (Wirth, 1951): **a**. Genitalia, aedeagus and parameres removed. **b**. Parameres. **c**. Aedeagus. *C. borkenti* sp. nov: **d**. Genitalia, aedeagus and parameres removed. **e**. Parameres. **f**. Aedeagus. *C. grogani* sp. nov. : **g**. Genitalia, aedeagus and parameres removed. **h**. Parameres. **i**. Aedeagus. Abbreviations: ALP = apicolateral point of epandrium; AP = apical point of aedeagus; BA = basal arch of aedeagus; CRC = cercus; GC = gonocoxite; GCA = gonocoxal apodeme; GNS = gonostylus; HI = hyaline incision of aedeagus; HYP = hypandrium; PA = paramere apex; PB = paramere base; PLP = posterolateral point of aedeagus. Scale bars = 100 μm.

Etymology

This species is named in honor of William L. Grogan Jr., who provided specimens for this project and guidance in my initial foray into ceratopogonid taxonomy.

Material examined

Holotype

USA • ♂; Oregon, Benton Co., 6 km NW of Corvallis; 3 Aug. 1989; M. Dietrich leg.; CNCI.

Paratypes

USA • 1 ♂, 1 ♀; same collection data as for holotype; CNCI • 1 ♂; California, Napa Co., N side of Howell Mountain, 2 mi. NNE of Angwin; 5–8 Jun. 1978; H.B. Leech leg.; USNM • 1 ♂; same collection data as for preceding; 7 Jun. 1978; USNM.

Description

Male

Measurements (n = 3). Head width 332–347(334); flagellomeres 48–50(49), 27–34(30), 27–34(29), 26–31(28), 24–31(29), 21–33(33), 27–37(34), 29–34(33), 35–39(37), 33–48(37), 99–115(111), 69–82(80), 80–93(81); AR 0.70–0.90(0.81); FR 1.74–1.83(1.83); wing length 1.21–1.29(1.24) mm; wing width 0.36–0.39(0.37) mm; costal ratio 0.48–0.55(0.55); GCR 1.73–2.33 (2.02); GSR 1.01–1.12(1.06); aedeagus ratio 2.3–2.46(2.4).

Thorax. Legs with femora and tibiae yellow or very lightly infuscate.

Genitalia (Fig. 9g–i). Distal portion of parameres tapering gradually to acute apex. Aedeagus broad posteriorly, tapering anteriorly; lateral margins forming a smooth, shallow arc, divergent posteriorly, curving outward to acute laterally directed posterolateral point at apex, forming a smooth concave arc medially to triangular posteriorly directed apical point; posterior margin weakly concave, hyaline medial incision broad posteriorly, tapering anteriorly.

Female

Measurements (n = 1). Head width 306; flagellomeres 32, 23, 26, 27, 32, 33, 36, 36, 48, 52, 61, 59, 68; AR 1.18; FR 1.74; wing length 1.42 mm; wing width 0.52 mm; costal ratio 0.52; spermathecal length 60; spermathecal width 49; spermathecal neck 11; spermatheca/neck ratio 0.17.

Thorax. Legs with hind femur infuscate, other femora and tibiae yellow.

Genitalia (Fig. 11e). 9th sternite anterior branch broadly triangular, apices rounded, widely separated; posterior branch broadly triangular, apex directed posteriorly, tip triangular with ridge along medial margin. 2 major spermathecae.

Distribution

California, Oregon (USA) (Fig. 13).

Remarks

This species belongs to the *C. moravicus* group. It can be differentiated from *C. moravicus* (Fig. 10h) and *C. aliciae* (Fig. 10e) by the aedeagus not conspicuously narrowing midway along its length, and from *C.* sp. M1 (Fig. 10c) and *C. propinquus* sp. nov. (Fig. 10k) by having the posterolateral point elongate and spiniform. It is readily distinguished from *C. borkenti* sp. nov. (Fig. 9f) by the weakly developed hyaline incision of the aedeagus. The female of this species is the most readily recognizable of any *Ceratoculicoides*, as the medial apex of the 9th sternite is only weakly concave, instead of deeply emarginate (Fig. 11e).

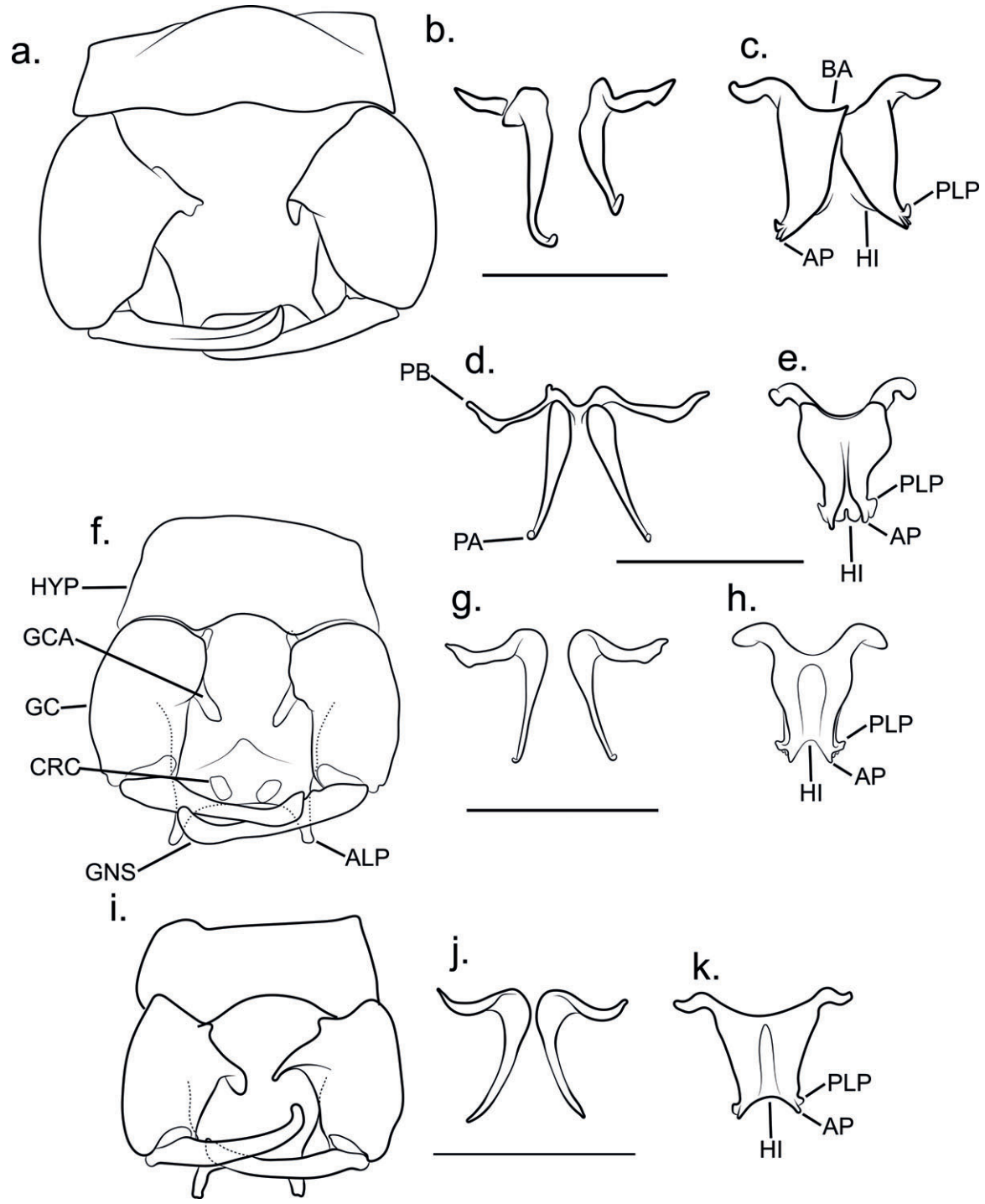

Fig. 10. Male genitalia III. *Ceratoculicoides* sp. M1: **a**. Genitalia, aedeagus and parameres removed. **b**. Parameres. **c**. Aedeagus. *C. aliciae* Huerta & Borkent, 2005: **d**. Parameres (adapted from Huerta & Borkent 2005). **e**. Aedeagus (adapted from Huerta & Borkent 2005). *C. moravicus* Knoz, 1987: **f**. Genitalia, aedeagus and parameres removed. **g**. Parameres. **h**. Aedeagus. *C. propinquus* sp. nov.: **i**. Genitalia, aedeagus and parameres removed. **j**. Parameres. **k**. Aedeagus. Abbreviations: ALP = apicolateral point of epandrium; AP = apical point of aedeagus; BA = basal arch of aedeagus; CRC = cercus; GC = gonocoxite; GCA = gonocoxal apodeme; GNS = gonostylus; HI = hyaline incision of aedeagus; HYP = hypandrium; PA = paramere apex; PB = paramere base; PLP = posterolateral point of aedeagus. Scale bars = 100 μm.

Ceratoculicoides moravicus Knoz, 1987
Figs 5b, 7e, 10f–h, 11f

Ceratoculicoides moravicus Knoz, 1987: 390, figs 1–19 (Czech Republic).

Ceratopogon (*Nilohelea*) *gracilipes* Remm, 1967: 27 (preoccupied name, subjective junior synonym), pl. 18, figs 1–7 (Georgia).
Ceratoculicoides havelkai Wirth & Grogan, 1988 (replacement name for *Ceratopogon gracilipes* Remm, subjective junior synonym). — Delécolle & Schiegg 1998: 274, figs 1–23.
Ceratoculicoides remmi Gosseries, 1988: 2 (replacement name for *Ceratopogon gracilipes* Remm, objective junior synonym of *C. havelkai* Wirth & Grogan).

Diagnosis

Male

Ceratoculicoides moravicus can be separated from congeners by the following combination of characters: femora and tibiae brown; wing length 1.1 mm, apices of parameres acute, tapering distally; aedeagus lateral margins straight basally, strongly tapered at midpoint, apical and posterolateral points adjacent, 1–2 accessory spines between apical point and posterolateral point of aedeagus, posterolateral point subtriangular, apex directed anteriorly (Fig. 10h).

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.62–1.83; femora and tibiae brown; wing length ~ 1.2 mm; single major spermatheca 75–77; medial margin of 9th sternite deeply concave.

Material examined

TURKEY • 1 ♀; Izmir, Bornova; May 1962; T. Curtin leg.; light, originally identified as *C. gracilipes*; CNCI • 1 ♂, 1 ♀; same collection data as for preceding; USNM.

Description

Male

Measurements (n = 1). Head width 289; flagellomeres 43, 27, 30, 29, 24, 25, 24, 32, 30, 36, 95, 76, 85; AR 0.85; FR 1.92; wing length 1.16 mm; wing width 0.37 mm; costal ratio 0.52; GCR 1.65; GSR 1.15; aedeagus ratio 1.33.

Thorax. Dorsocentral punctations possibly absent, at most a few spots of thinned cuticle among dorsocentral setae. Legs with femora and tibiae brown.

Genitalia (Fig. 10f–h). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins tapering, constricted noticeably at midlength; posterior margin a smooth concave arc, hyaline medial incision broad posteriorly, tapering anteriorly; base of posterolateral point directed laterally, apex rounded, directed anterolaterally; apical point subacute, directed posterolaterally, adjacent to posterolateral point, with 1–2 accessory spines between apical and posterolateral points, similar in size and shape to apical point.

Female

Measurements (n = 2). Head width 272–314; flagellomeres 33–41, 23–27, 21–25, 26–32, 26–32, 28–30, 31, 33–34, 46–50, 48–51, 54–55, 51–53, 62–63; AR 1.11–1.14; FR 1.62–1.83; wing length 1.25–1.28 mm; wing width 0.48–0.5 mm; costal ratio 0.52–0.54; spermathecal length 75–77; spermathecal width 66–70; spermathecal neck (n = 1) 11; spermatheca/neck ratio (n = 1) 0.14.

Thorax. Legs with femora and tibiae brown.

Genitalia (Fig. 11f). 9th sternite anterior branch broad, evenly rounded, apices nearly touching medially; posterior branch directed straight posteromedially without curve, spiniform, weakly tapering, tip pointed or with minute hook at apex. 1 major spermatheca.

Distribution

Western Palaearctic.

Remarks

This extralimital species is diagnosed here to aid in differentiating it from other members of the *C. moravicus* group, particularly *C.* sp. M1 (see above). Delécolle & Schiegg synonymized *C. havelkai* and *C. moravicus* without examining either holotype, based solely on specimens from Switzerland and Germany (Delécolle & Schiegg 1998). Any future work on the Palaearctic fauna should involve examining both type specimens to confirm they are conspecific. Females of this species are the only known *Ceratoculicoides* with a single major spermatheca. The males are extremely similar to those of *C. aliciae*, *C. propinquus* sp. nov. and *C.* sp. M1. *Ceratoculicoides moravicus* (Fig. 10h) can be distinguished from *C. aliciae* (Fig. 10e) by the posterior margin of the aedeagus being evenly concave (vs with acute medial notch), from *C. propinquus* (Fig. 10k) by the accessory spines between the apical and posterolateral points (spines absent in *C. propinquus*), and *C.* sp. M1 (Fig. 10c) by having the aedeagus tapering distinctly at midlength (vs lateral margins straight). The differences between *C. moravicus* and *C.* sp. M1 may be the result of the overly compressed slide preparation of that specimen. Additional material is needed to ascertain whether the latter provisional morphospecies is conspecific.

Ceratoculicoides propinquus sp. nov.
urn:lsid:zoobank.org:act:E8A43CD5-482E-4376-8AAB-FBC676694752
Figs 5c, 10i–k

Diagnosis

Male

Ceratoculicoides propinquus sp. nov. can be separated from congeners by the following combination of characters: femora and tibiae brown; wing length ~0.95 mm; apices of parameres acute, tapering distally; aedeagus lateral margins straight, apical and posterolateral points adjacent, without accessory spines, posterolateral point subtriangular, apex directed anteriorly (Fig. 10k).

Female

Unknown.

Etymology

The specific epithet '*propinquus*' is a Latin adjective expressing 'closeness' or 'kinship', which refers to the similarity of this species with *C.* sp. M1 and *C. moravicus*.

Material examined

Holotype

USA • ♂; California, Los Angeles Co., Pine Canyon; 13 Jun. 1953; W.A. McDonald leg.; USNM.

Paratype

CANADA • ♂; British Columbia, 23 km NW of Port Renfrew, Upper Carmanah Valley; 16–30 Aug. 1991; N. Winchester leg.; CNCI.

Description (male)

Measurements (n = 2). Head width 270–286; flagellomeres 44–47, 21–26, 21–25, 25, 21–22, 19–22, 22–23, 27–30, 27–28, 29–32, 77, 51–63, 64–71; AR 0.74–0.76; FR 1.68–1.7; wing length 0.94–0.96 mm; wing width 0.29–0.31; costal ratio 0.53; GCR 1.58–1.7; GSR 1.04–1.05; aedeagus ratio 1.26–1.35.

Thorax. Dorsocentral punctations possibly absent, at most a few spots of thinned cuticle among dorsocentral setae. Legs with femora and tibiae yellow or very lightly infuscate.

Genitalia (Fig. 10i–k). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins straight, becoming slightly divergent at apex; posterior margin a smooth concave arc, hyaline medial incision broadest posteriorly, tapering anteriorly; base of posterolateral point directed laterally, apex rounded, directed anterolaterally; apical point subacute, directed posterolaterally, adjacent to posterolateral point, without accessory spines between apical and posterolateral points, similar in size and shape to apical point.

Distribution

British Columbia (Canada), California (USA) (Fig. 13).

Remarks

This species belongs to the *C. moravicus* group, and is very similar to *C. aliciae*, *C.* sp. M1 and *C. moravicus*. It can be recognized by the straight lateral margins of the aedeagus (vs distinctly tapering at midlength in *C. aliciae* and *C. moravicus*) and the apical and posterolateral points being adjacent but without accessory spines between them (spines present in *C.* sp. M1 and *C. moravicus*), and the posterolateral point apex rounded and directed anteriorly (Fig. 10k). The posterior margin of the aedeagus forms an evenly concave arc, while *C. aliciae* has a distinct acute medial notch along its posterior margin (Fig. 10e). Females have not been associated for this species.

Ceratoculicoides sp. M1
Figs 5a, 10a–c

Diagnosis

Male

It can be separated from congeners by the following combination of characters: femora and tibiae brown; wing length 1.2 mm; apices of parameres acute, tapering distally; aedeagus lateral margins straight, apical and posterolateral points adjacent, 1–2 accessory spines between apical point and posterolateral point of aedeagus, posterolateral point subtriangular, apex directed anteriorly (Fig. 10c).

Female

Unknown.

Material examined

USA • 1 ♂; California, San Bernardino Co., Death Valley National Park, Saratoga Springs; 19 Mar. 1955; McDonald leg.; USNM.

Description (male)

Measurements (n = 1). Head width unknown (head of specimen mounted in profile); flagellomeres 68, 31, 32, 30, 29, 27, 29, 25, 32, 44, 103, 73, 73; AR 0.72; FR unknown; wing length 1.26 mm; wing width 0.4 mm; costal ratio 0.54; GCR 1.65; GSR 0.92; aedeagus ratio 1.17.

Thorax. Dorsocentral punctations possibly absent, at most a few spots of thinned cuticle among dorsocentral setae. Legs with femora and tibiae brown.

Genitalia (Fig. 10a–c). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins straight, becoming slightly divergent at apex; posterior margin a smooth concave arc, hyaline medial incision broad posteriorly, tapering anteriorly; base of posterolateral point directed laterally, apex rounded, directed anterolaterally; apical point subacute, directed posterolaterally, adjacent to posterolateral point, with 1–2 accessory spines between apical and posterolateral points, similar in size and shape to apical point.

Distribution

California (USA) (Fig. 13).

Remarks

This is a provisional male morphospecies (not a formal binomen), as there is some evidence this may be the male of *C. longipennis* (see taxonomic note for that species). The genitalia of the only specimen were heavily compressed during mounting, splitting the aedeagus and distorting other structures, complicating its comparison with similar species. This morphospecies belongs to the *C. moravicus* group based on having the aedeagus lateral margins mostly straight and a concave posterior margin, deep hyaline medial incision, and the dorsolateral and apical points of the aedeagus adjacent at the posterolateral corner of the aedeagus. *Ceratoculicoides* sp. M1 (Fig. 10c) lacks the extensive subtrapezoidal medial incision of *C. borkenti* sp. nov. (Fig. 9f), while this species can be separated from *C. grogani* sp. nov. (Fig. 9i) by the posterolateral point length being subequal to its basal width (vs much longer than its basal width) and the apex of the posterolateral point is directed anterolaterally (vs slightly posterolaterally). It is distinguished from *C. propinquus* sp. nov. (Fig. 10k) by the presence of accessory spines between the apical and posterolateral points of the aedeagus, and larger adult size (1.25 mm wing length). It can be differentiated from the very similar *C. aliciae* (Fig. 10e) and *C. moravicus* (Fig. 10h) by the lateral margins of the aedeagus being relatively straight, weakly expanding apically (vs distinctly narrowing about midway along their length in those two species) and the emargination at the posterior apex of the aedeagus is much broader. However, it is possible that these differences result from the amount of compression the specimen experienced during slide mounting, as the aedeagus is partially split medially. *Ceratoculicoides aliciae* is smaller (male wing length 0.93 mm) than *C.* sp. M1 (suggesting its distinctness), but it is possible that *C. moravicus* is conspecific with *C.* sp. M1. This needs to be resolved by examining additional uncompressed specimens.

Other Ceratoculicoides species

Ceratoculicoides confusus sp. nov.
urn:lsid:zoobank.org:act:71C1E0FF-3BE9-46F1-8121-8D3C237262D6
Figs 4a, c, 6a, 8a–f, 11c–d

non *Ceratoculicoides longipennis* – sensu Wirth & Ratanaworabhan 1971: 172 (incorrect assignment of male adult), fig. 1. — Wirth & Grogan 1988: 116, fig. 16.

Diagnosis

Male

Ceratoculicoides confusus sp. nov. can be separated from congeners by the following combination of characters: femora and tibiae brown, apices of parameres acute, tapering distally; aedeagus lateral and posterior margins convex, medial apex of aedeagus without hyaline incision, apical points absent,

posterolateral points spiniform, emerging from dorsal surface of aedeagus, apex curving posterior, < 0.25 times width of apex of aedeagus (Fig. 8c, f).

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.37–1.64; femora and tibiae brown, wing length 1.2–1.5 mm; 2 major spermathecae, largest 99–105; medial margin of 9th sternite deeply concave.

Etymology

'*Confusus*' is the Latin participle for 'confusion', in reference to the past misapplication of the name *C. longipennis* to this species.

Material examined

Holotype

CANADA • ♂; Nova Scotia, Victoria Co., Baddeck; Jul. 1971; G.B. Fairchild leg.; black light trap; CNCI.

Paratypes

CANADA • 3 ♀♀; New Brunswick, Kent Co., Kouchibouguac National Park; 2–13 Jul. 1977; J.R. Vockeroth leg.; CNCI • 1 ♂; Quebec, Outaouais Region, Masham, Duncan Lake; 7 Jun. 1985; K. Mikkola leg.; CNCI.

USA • 1 ♂; Georgia, Murray Co., Fort Mountain State Park; 11 Jun. 1968; R.E. Woodruff leg.; USNM • 1 ♀; Maryland, Prince Georges Co., College Park; 12 May 1975; W.L. Grogan Jr. leg.; light trap; FSCA • 1 ♂, 1 ♀; New York, Cattaraugus Co., Alleghany State Park; 28 May–3 Jun. 1963; W.W. Wirth leg.; stream margin; FSCA • 1 ♂; North Carolina, Macon Co., Highlands, Wightman Cottage; 5 Jul. 1987; W.W. Wirth leg.; UV light trap; USNM • 1 ♀; Tennessee, Sevier Co., Clingman's Dome, Great Smoky Mountain National Park, ATBI Plot; 16–29 Aug. 2001; Parker, Stocks and Petersen leg.; FSCA.

Other material

COLOMBIA • 1 ♂; Vichada, PNN Tuparro, Bosque Sabana; 5.35° N, 67.85° W; 29 Nov.–8 Dec. 2000; W. Villalba leg.; CNCI.

Description

Male

Measurements (n = 4) [Colombian specimen in brackets]. Head width (n = 3) 308–345(322) [315]; flagellomeres (n = 2) 41–58 [49], 24–34 [29], 28–30 [25], 25–30 [30], 24–27 [26], 23–30 [28], 17–31 [26], 24–31 [29], 20–35 [28], 25–38 [34], 97–99 [83], 63–68 [67], 79 [66]; AR 0.81–0.93 [0.71]; FR (n = 1) 1.71 [1.65]; wing length 0.95–1.16(1.09) [0.98] mm; wing width 0.29–0.38(0.32) [0.30] mm; costal ratio (n = 1) 0.53 [0.54]; GCR (n = 2) 1.56–2.0 [1.7]; GSR (n = 2) 0.93–1.0 [1.12]; aedeagus ratio (n = 2) 0.75–0.84 [0.81].

Thorax. Dorsocentral punctations inconspicuous, present among posterior third of dorsocentral setae, may be absent in some specimens. Legs with femora and tibiae brown.

Genitalia (Fig. 8a–f). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins convex, rounded, seamlessly transitioning into rounded posterior margin, medial apex without notch or hyaline incision; posterolateral point a posteriorly directed, hooked acute spine on dorsal surface of posterolateral margin.

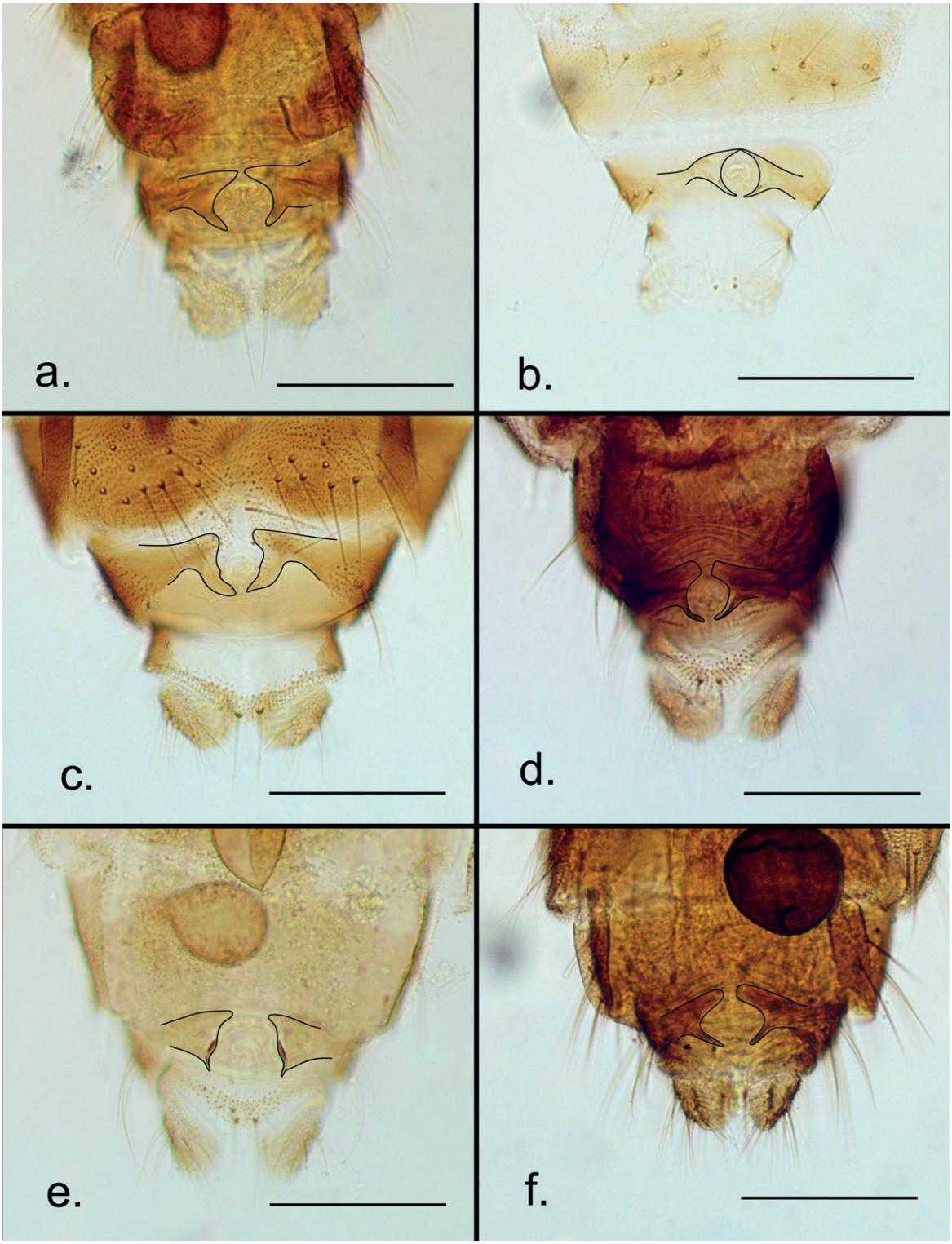

Fig. 11. Female sternite 9 I. **a**. *Ceratoculicoides aliciae* Huerta & Borkent, 2005, paratype, Chamela Biological Station, Jalisco, Mexico. **b**. *C. borkenti* sp. nov., paratype, Nogales, Arizona, USA. **c**. *C. confusus* Kouchibouguac National Park, New Brunswick, Canada. **d**. *C. confusus*, paratype, Great Smoky Mountains National Park, Tennessee, USA. **e**. *C. grogani* sp. nov., paratype, Corvallis, Oregon, USA. **f**. *C. moravicus* Bornova, Izmir, Turkey. Linework has been added to make sternite 9 easier to discern. Scale bars = 100 μm.

Female

Measurements (n = 4). Head width (n = 3) 317–352(336); flagellomeres (n = 3) 31–36(35), 23–26(24), 25–28(25), 25–30(28), 27–30(30), 28–33(29), 28–35(32), 27–35(35), 44–54(52), 46–55(51), 46–59(55), 51–62(56), 60–72(66); AR 1.15–1.2(1.17); FR 1.37–1.64(1.57); wing length 1.26–1.45(1.41) mm; wing width 0.49–0.59(0.55) mm; costal ratio (n=1) 0.58; spermathecal length 99–105(102); spermathecal width 76–86(77); spermathecal neck 18–28(24); spermatheca/neck ratio 0.23.

Thorax. Legs with femora and tibiae brown.

Genitalia (Fig. 11c–d). 9th sternite anterior branch truncate, apices widely separated; base of posterior branch directed posteriorly, distal half curving medially, tip rounded. 2 major spermathecae.

Distribution

Eastern North America (Canada and USA); Vichada (Colombia) (Fig. 13b–c).

Remarks

The male of this species was described as *C. longipennis* in Wirth & Ratanaworabhan (1971). It appears Wirth & Ratanaworabhan conflated three species in their description of *C. longipennis*, assigning female specimens with large spermathecae from the Pacific Northwest with *C. longipennis* based on wing length, then associating this eastern male morphospecies to *C. longipennis* based on the large spermathecae found in the females. The females associated with this eastern morphospecies are consistently smaller than the holotype of *C. longipennis*, with wing lengths less than 1.5 mm (vs 1.6 in said holotype); thus, the aforementioned male morphospecies represents a new taxon, *C. confusus*. Subsequent publication records of *C. longipennis* from eastern North America (Wilkening *et al.* 1985) represent this species. Female *C. confusus* can be recognized by being the only known species in eastern North America with a spermathecal length >80 μm. Only the western *C. pacificus* has similarly sized spermathecae, but it has wing lengths over 1.5 mm, while the female of *C. confusus* has a wing length between 1.2 and 1.5 mm. The males of this species can be distinguished by the convex lateral and posterior margins of the aedeagus, lack of a hyaline incision along the posterior margin, and absence of apical points (Fig. 8c).

I have assigned a male specimen from Colombia to this species based on its essentially identical genitalia features. The other morphological characters of this male fit within the range of North American material (the measurements of this specimen are included in brackets after the North American material in the description), although the dorsocentral punctations are more numerous and the antennal ratio is smaller than in the Nearctic specimens. I have also examined two females from the same locality (see Unassociated *Ceratoculicoides* female *Ceratoculicoides* specimens below), each apparently belonging to a separate species based on their wing lengths and the size of their spermathecae (*C.* sp. F1 with 1.25 mm wing length and 62 μm spermatheca length vs *C.* sp. F2 with 0.95 mm wing length and 76 μm spermatheca length). I do not feel confident associating either of these female morphospecies with the male based on the currently available material. If either of these female species is conspecific with this Colombian male, it would require reassessment of the species characters and boundaries of *C. confusus*.

Ceratoculicoides longipennis (Wirth, 1952)

Helea longipennis Wirth, 1952: 201 (original description).

Ceratopogon (*Nilohelea*) *longipennis* – Wirth 1965: 133 (combination, in catalog).

Ceratoculicoides longipennis – Wirth & Ratanaworabhan 1971: 172 (combination, redescription of female). — Knoz 1987: 391 (key). — Wirth & Grogan 1988: 116 (incorrect application of name to fig. 16). — Borkent & Wirth 1997: 95 (in catalog). — Huerta & Borkent 2005: 114 (catalog). — Borkent & Grogan 2009 (in catalog). — Borkent & Dominiak 2020: 157 (in catalog).

Diagnosis

Male

Unknown.

Female

Femora and tibiae brown, wing length 1.6 mm.

Material examined

Holotype

USA • ♀; California, Tulare Co., Sequoia National Park, Stony Brook; 13 Jul. 1947; W.W. Wirth leg.; USNM.

Paratype

USA • 1 ♀; California, Tulare Co., Lemon Cove, Kaweah River; 4 Jul. 1947; W.W. Wirth leg.; USNM; (not conspecific with holotype, see taxonomic notes).

Distribution

California (USA).

Remarks

There has been considerable confusion with the identity of this species, as the holotype is a female described in Wirth's (1952) monograph of the California Ceratopogonidae. Wirth & Ratanaworabhan (1971) asserted that this species was conspecific with a morphospecies from eastern North America based primarily on the size of their spermathecae. Based on their material examined list, Wirth & Ratanaworabhan did not have access to any male specimens from California or nearby states. The broader range of material I have been able to examine demonstrates that the eastern morphospecies is not *C. longipennis* (described above as *C. confusus*). My comparison of the paratype and holotype of *C. longipennis* also found they are not conspecific, with the paratype having a wing length of 1 mm, while the holotype wing length is 1.6 mm. While Wirth & Ratanaworabhan described large (75–82 μm) spermathecae for this species, they never dissected or slide mounted the holotype. It appears from their material examined and my work in the USNM collection that they measured slide mounted females from Oregon and Washington belonging to *C. pacificus* as part of their description. I have not dissected the *C. longipennis* holotype to ascertain the size of its spermathecae, as I did not realize the depth of confusion surrounding the identity of this species when I had access to it. Even dissecting the holotype would offer few clues to the identification of this species based on the information currently available, as there are only a handful of characters which offer any diagnostic utility, and many female specimens are currently unplaceable to species (see Discussion).

Females of *C. pacificus* match the *C. longipennis* holotype in wing length, but they are known only from temperate rainforests in British Colombia, Oregon, and Washington. The nearest locality of this species is in the Willamette Valley of Oregon, over 900 km from the type locality in the Sierra Nevada Range. In the USNM collection, I found a specimen of a male morphospecies from Death Valley National Park, California, which fits the large size (~1.25 mm wing length) expected for the

male of *C. longipennis*. As size and loose geographic proximity are extremely weak evidence upon which to base an association, I have treated this male species as *Ceratoculicoides* sp. M1 above. Since the holotype remains entire and pinned, it may be possible to sequence its molecular barcode to associate it with future specimens. However, if additional material and further study deprecates the diagnosability of the holotype, it may be necessary to petition the International Commission of Zoological Nomenclature to set aside the holotype and designate a male neotype for *C. longipennis* (under article 75.5, ICZN 1999).

Ceratoculicoides pacificus sp. nov.
urn:lsid:zoobank.org:act:8C193FC1-C09F-4305-9EC8-17544078662A
Figs 1–3, 4b, 6c, 8g–i, 12a–b

Diagnosis

Male

Ceratoculicoides pacificus sp. nov. can be separated from congeners by the following combination of characters: femora and tibiae brown; apices of parameres acute, tapering distally; aedeagus lateral margins convex, medial apex of aedeagus with hyaline incision, posterolateral spines elongate, 0.5 width of apex of aedeagus (Fig. 8i).

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.62–1.72; femora and tibiae brown, wing length 1.5–1.8 mm; 2 major spermathecae, largest 88–96; medial margin of 9th sternite deeply concave.

Etymology

The specific epithet '*pacificus*' is a Latin adjective referring to 'peacemaking' or 'peacefulness'. This epithet is in reference to this species inhabiting the coastal Pacific Northwest region.

Material examined

Holotype

CANADA • ♂; British Columbia, Cowichan District, 23 km NW of Port Renfrew, Upper Carmanah Valley; 21 Jun.–3 Jul. 1991; N. Winchester leg.; CNCI.

Paratypes

CANADA • 10 ♂♂, 2 ♀♀; same collection data as for holotype; CNCI • 3 ♂♂, 1 ♀; same collection data as for holotype; 4–15 Jul. 1991; CNCI • 3 ♀♀; same collection data as for holotype; 31 Jul.–11 Aug. 1991; CNCI.

Other material

CANADA – **British Columbia** • 1 ♀; East Sooke Pk. 20 km SW of Victoria; 31 Jul.–14 Aug. 1984; R. A. Cannings leg.; CNCI • 1 ♂; same collection data as for preceding; 29 Jun.–18 Jul. 1989; A. Borkent leg.; CNCI • 1 ♀; same collection data as for preceding; 18–26 Jul. 1989; CNCI • 1 ♂; same collection data as for preceding; 12.5 km NW of Gold River, coll. A. Borkent; 18 Jul. 1991; CNCI • 2 ♀♀; Lake Cowichan; 26 Jul. 1979; J. Smith leg.; CNCI • 1 ♂; 25 km W of Lake Cowichan; 8 Jul. 1991; A. Borkent leg.; CNCI • 1 ♂; 33 km NW of Lake Cowichan; 9 Jul. 1991; A. Borkent leg.; CNCI • 2 ♀♀; 2.3 km NW of Lake Cowichan, South Shore Rd.; 19–28 Jul. 1985; I. M. Smith leg.; CNCI • 1 ♀; 5 km NE of Port Renfrew; 8 Jul. 1991; A. Borkent leg.; CNCI • 1 ♂; Ucluelet; 15–20 Jul. 1979; I. M. Smith leg.; CNCI.

USA • 1 ♂; Oregon, Benton Co., Mary's Peak, 21 km NW of Corvallis; 19 Jul. 1985; A. Borkent leg.; CNCI • 1 ♂; Washington, Kittatas Co., Okanagan-Wenatchee National Forest, DeRoux Forest Campground; 11 Aug. 1971; Goeden and Gurney leg.; light trap; originally identified as *C. longipennis*; USNM • 1 ♂, 1 ♀; same collection data as for preceding; Olympic National Park; CNCI.

Description

Male

Measurements (n = 5). Head width 327–349(339); flagellomeres 49–53(51), 29–36(32), 26–30(27), 21–33(29), 25–29(28), 27–30(30), 25–31(29), 27–30(30), 30–35(32), 29–37(33), 84–102(96), 66–75(71), 79–88(81); AR 0.89–1.02(1.00); FR (n = 1) 1.67; wing length 1.14–1.34(1.22) mm; wing width 0.37–0.45(0.42) mm; costal ratio (n = 1) 0.50; GCR 2.1–2.2(2.1); GSR 1.0–1.1(1.1); aedeagus ratio 0.83–1.0(0.91).

Thorax. Dorsocentral punctations prominent and interspersed in posterior half of dorsocentral setae. Legs with femora and tibiae brown.

Genitalia (Fig. 8g–i). Distal portion of parameres tapering gradually to acute apex. Aedeagus lateral margins convex, rounded, posterior margin convex, tapering posteriorly to medial notch and acute hyaline incision; elongate acute posterolateral point at transition of posterior and lateral margin, spine length 0.5 times width of aedeagus; posteriorly directed apical point adjacent to medial notch.

Female

Measurements (n = 5). Head width (n = 3) 310–360(343); flagellomeres (n = 3) 37–43(40), 23–27(23), 27–29(29), 29–32(30), 32–36(36), 32–36(33), 34–38(37), 36–38(38), 51–57(56), 50–53(53), 58–63(60), 55–62(56), 69–76(72); AR 0.73–0.82(0.78); FR 1.62–1.72(1.65); wing length 1.57–1.84(1.63) mm; wing width 0.6–0.64(0.62) mm; costal ratio (n = 1) 0.53; spermathecal length 88–96(93); spermathecal width 80–91(81); spermathecal neck 16–26(23); spermatheca/neck ratio 0.24.

Thorax. Legs with femora and tibiae brown.

Genitalia (Fig. 12a–b). 9th sternite anterior branch truncate, apices widely separated; base of posterior branch directed posteriorly, distal half curving medially, tip usually rounded, sometimes with a minute hook at apex. 2 major spermathecae.

Distribution

British Columbia (Canada), California, Oregon, Washington (USA).

Remarks

Females of this species are similar in size to the female holotype of *C. longipennis*, but the geographic disjunction between the type locality and the range of *C. pacificus* argues against their conspecificity. I believe that the stability of nomenclature is better served by describing this taxon under a new name rather than assigning this morphospecies to *C. longipennis* based on spurious evidence, especially as another male morphospecies, sp. M1, has as much or more evidence suggesting it is the male of *C. longipennis*. Females of this species are the only *Ceratoculicoides* in western North America with spermathecae >80 μm long, but the other regional females are poorly known and this character may not be diagnostic. Males can be distinguished from all other *Ceratoculicoides* by their aedeagus having convex lateral and posterior margins, long (>0.5× width of main body of the aedeagus) posterolateral points, and acute hyaline medial incision flanked by short triangular apical points well separated from the posterolateral points (Fig. 8i).

Ceratoculicoides virginianus (Wirth, 1951)
Figs 4d, 6d, 9a–c, 12c

Helea (*Isohelea*) *virginiana* Wirth 1951: 318 (original description), fig. 5.
Ceratoculicoides blantoni With & Ratanaworabhan, 1971: 172 (original description), fig. 2. **Syn. nov.**

Ceratopogon (*Nilohelea*) *virginianus* – Wirth 1965: 133 (combination, in catalog).
Ceratoculicoides virginianus – Wirth & Ratanaworabhan 1971: 172 (redescription), fig. 3. — Knoz 1987: 391 (key). — Borkent & Wirth 1997: 95 (in catalog). — Huerta & Borkent 2005: 114 (catalog). — Borkent & Grogan 2009 (in catalog). — Borkent & Dominiak 2020: 157 (in catalog).
Ceratoculicoides blantoni – Knoz 1987: 391 (key). — Borkent & Wirth 1997: 95 (in catalog). — Huerta & Borkent 2005: 114 (catalog). — Borkent & Grogan 2009 (in catalog). — Borkent & Dominiak 2020: 157 (in catalog).

Diagnosis

Male

Ceratoculicoides virginianus can be separated from congeners by the following combination of characters: femora and tibiae yellow or brown; apices of paramere broadly rounded, not tapering, minute apical point displaced laterally; aedeagus subquadrate, slightly constricted apically (Fig. 9b–c).

Female

Only species of *Ceratoculicoides* with the following combination of characters: FR 1.57–1.75; femora and tibiae yellow or brown, wing length ~0.9–1.3 mm; 2 major spermathecae, largest 52–69; medial margin of 9th sternite deeply concave.

Material examined

Holotype

USA • ♂; Virginia, Augusta Co., Mount Solon; 11 Jul. 1950; W.W. Wirth leg.; USNM.

Other material

CANADA • 1 ♀; Ontario, Elgin Co., Springwater Conservation Area; 9 Jul. 1984; A. Borkent leg.; CNCI • 1 ♂; Quebec, Outaouais Region, Gatineau Park, Black Lake; 27 Jun. 1985; L. Forster leg.; originally identified as *C. blantoni*; CNCI.

USA • – **Florida** 1 ♂; Alachua Co., Gainesville; 20 Apr. 1967; W.W. Wirth leg.; USNM • 1 ♀; Levy Co., Yankeetown; 21 Jan. 1983; A. Wilkening leg.; light trap with CO_2; originally identified as *C. blantoni*; FSCA • 1 ♂; Liberty Co. Torreya State Park; 15 May 1971; G.B. Fairchild and B.L. Trap leg.; USNM • 1 ♂; Wakulla Co., Sopchoppy; 13–14 May 1979; J.A. Downes; CNCI – **Maryland** • 2 ♂♂; Prince Georges Co., Patuxent Wildlife Research Center; 28 Apr. 1976; W.L. Grogan leg.; originally identified as *C. blantoni*; FSCA • 1 ♀; 6 May 1976; originally identified as *C. blantoni*; FSCA • 1 ♂; Patuxent Wildlife Refuge; 10 May 1978; W.W. Wirth leg.; originally identified as *C. blantoni*; USNM • 1 ♂; 12 May 1979; originally identified as *C. blantoni*; USNM • 1 ♀; Wicomico Co., Salisbury; 15–21 May 1979; W.L. Grogan leg.; Malaise trap; FSCA • 1 ♂ (holotype of *C. blantoni*); Worcester Co., Snow Hill; 19 May 1968; W.H. Anderson leg.; USNM – **North Carolina** • 1 ♂; Jackson Co., Dunaley bog, 7 mi S of Cashiers; 18 Jun. 1986; W.W. Wirth leg.; USNM • 1 ♂; Macon Co., Highlands, Wightman Cottage; 21 Jun. 1986; W.W. Wirth leg.; USNM • 1 ♀; Highlands; 3 Jun. 1957; J.R. Vockeroth leg.; CNCI – **Virginia** • 1 ♂; Falls Church [independent city]; 4 May 1959; W.W. Wirth leg.; originally identified as *C. blantoni*; USNM • 1 ♂; 7 May 1960; originally identified as *C. blantoni*; USNM • 1 ♂; Falls Church, Holmes Run; May 1962; W.W. Wirth leg.; originally identified as *C. blantoni*; USNM.

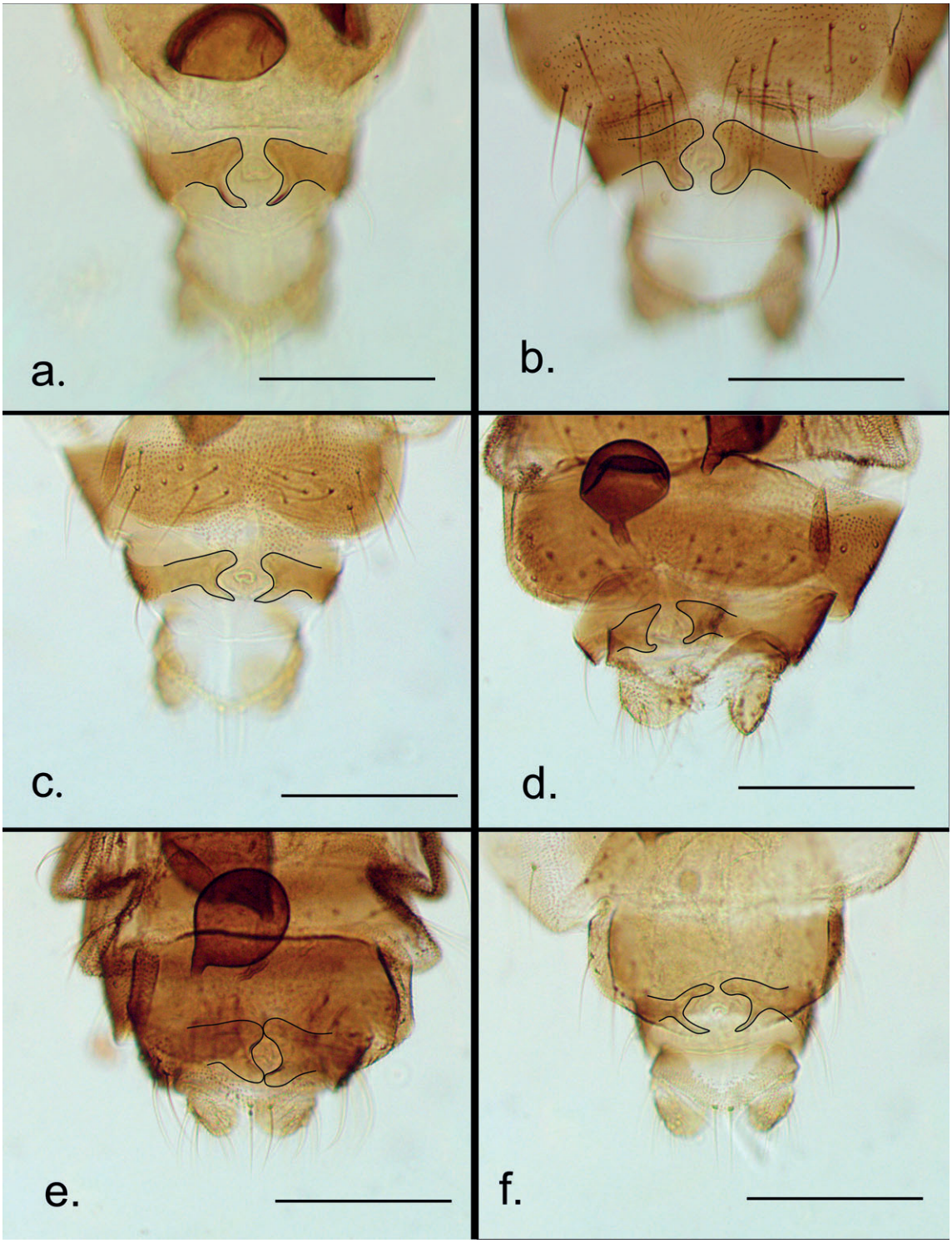

Fig. 12. Female sternite 9 II. **a**. *Ceratoculicoides pacificus* sp. nov., paratype (CNCI), Carmanah Valley, British Columbia, Canada. **b**. *C. pacificus* paratype (CNCI), East Sooke Peak, British Columbia, Canada. **c**. *C. virginianus* (Wirth, 1951), Springwater Conservation Area, Ontario, Canada. **d**. *Ceratoculicoides* sp. F1, Tuparro National Park, Colombia. **e**. *Ceratoculicoides* sp. F2, Tuparro National Park, Colombia. **f**. *Ceratoculicoides* sp. F3, Rincon, Costa Rica. Linework has been added to make sternite 9 easier to discern. Scale bars = 100 μm.

Description

Male

Measurements (n = 3). Head width 282–295(289); flagellomeres 50–54(52), 25–30(28), 22–31(26), 25–28(26), 21–27(25), 22–32(26), 24–28(26), 23–36(27), 29–33(32), 26–37(28), 81–114(103), 63–77(69), 51–69(59); AR 0.74–0.8(0.75); FR 1.63; wing length (n = 10) 0.81–1.21(1.04); wing width (n = 10) 0.25–0.4(0.34); costal ratio (n = 1) 0.49; GCR 1.87–2.17(2.08); GSR 0.97–1.14(1.08); aedeagus ratio 0.66–0.91(0.78).

Thorax. Dorsocentral punctations prominent and interspersed in posterior half of dorsocentral setae. Legs with femora and tibiae yellow or brown.

Genitalia (Fig. 9a–c). Distal portion of parameres not tapered, apex broadly rounded, with small subacute point displaced laterally. Aedeagus lateral margins convex, rounded, posterior margin straight, notched medially without hyaline incision, posterolateral point triangular, shifted medially nearly to lateral margin of medial notch, curving smoothly into dorsally directed, acute apical point.

Female

Measurements (n = 5). Head width (n = 3) 267–306(274); flagellomeres (n = 3) 27–30(27), 17–25(18), 18–25(22), 23–28(26), 24–32(28), 24–32(27), 23–32(31), 24–37(31), 42–52(47), 44–50(47), 48–54(52, 50–54(54), 55–70(66); AR 1.15–1.33(1.29); FR 1.57–1.75(1.69); wing length (n = 6) 0.92–1.29(1.19); wing width (n = 6) 0.34–0.49(0.45); costal ratio 0.56; spermathecal length 52–69(64); spermathecal width 37–56(47); spermathecal neck 12–23(19); spermatheca/neck ratio 0.3.

Thorax. Legs with femora and tibiae yellow or brown.

Genitalia (Fig. 12c). 9th sternite anterior branch truncate or obtusely rounded, apices widely separated; base of posterior branch directed posteriorly, distal half curving medially, tip rounded or pointed. 2 major spermathecae.

Distribution

Eastern North America (Canada and USA) (Fig. 13).

Remarks

Wirth & Ratanaworabhan (1971) described *C. blantoni*, distinguishing it from *C. virginianus* based on leg coloration (brown in *C. blantoni*, yellow in *C. virginianus*), orientation of the apex of the paramere (posterolateral in *C. blantoni*, ventroposterior in *C. virginianus*), and the aedeagal proportions (broader than long in *C. blantoni*, as long as broad in *C. virginianus*). My examination of additional material of both species found that these characters are not diagnostic. Leg color appears to be a spectrum; while some specimens have completely yellow and others completely brown legs, there are intermediates with solid brown femora and yellow tibiae or femora proximally brown and yellow distally. The legs of the holotype of *C. blantoni* are now yellow with brown bands on the femora, probably a result of the slide mounting process. The male genitalia characters used by Wirth & Ratanaworabhan appear to be artifacts of slide mounting. Specifically, the direction of the apex of the parameres is directly correlated to the compression of the genitalia by the coverslip during mounting: when there is little pressure the parameres point ventroposteriorly, but when compressed the apices are displaced laterally. The proportions of the aedeagus are similarly affected by the mounting of the specimen, the degree of tilt of the aedeagus in the dorsal plane changes its apparent proportions on the slide mount due to foreshortening. As no characters consistently separate *C. blantoni* from *C. virginianus*, *C. blantoni* is here considered a junior synonym of the latter species.

Currently, females of this species can be recognized by being the only known species in eastern North America with spermathecae < 70 μm long. There are several morphospecies from the western Nearctic

and Neotropics with similarly sized spermathecae. *Ceratoculicoides virginianus* (Fig. 12c) can be separated from *C. grogani* sp. nov. by the deeply concave and rounded medial margin of the 9th sternite (vs weakly concave and sinuous, Fig. 11e), the base of the posterior branch being posteriorly from the base, curving medially in its apical half (vs directed posteromedially in an even curve in *C. borkenti*, Fig. 11b), the posterior branch tapering only in its apical half (vs *C. borkenti* sp. nov. and *C.* sp. F3 where it tapers to an acute spine in the basal half, Figs 11b, 12f). Accordingly, *C. virginianus* cannot be distinguished from *C.* sp. F1 based on morphology from our current knowledge. There is some variability in the shape of the apices of the anterior and posterior branches of the 9th sternite. The anterior branch can be obtusely rounded or somewhat flattened and truncate, while the tip of the posterior branch may be either pointed or acutely rounded. Males can be separated from all other *Ceratoculicoides* by the broadly rounded apex of the paramere with subacute triangular point (Fig. 9b), the aedeagus with convex lateral margins, no hyaline medial incision, and the dorsolateral and apical points directed dorsally (Fig. 9c).

Provisional female taxa

Ceratoculicoides sp. F1
Fig. 12d

Diagnosis

Male

Currently unknown.

Female

Only species of *Ceratoculicoides* with the following combination of characters: femora and tibiae yellow, wing length ~1.2 mm; 2 major spermathecae, largest 56–66; medial margin of 9th sternite deeply concave.

Material examined

COLOMBIA • 1 ♀; Magdalena, Sierra Nevada de Santa Marta National Park, El Ramo; 10.8° N, 73.65° W; 15 Oct.–1 Nov. 2000; J. Cantillo leg.; CNCI • 1 ♀; Vichada, PNN Tuparro, Bosque Sabana; 5.35° N, 67.85° W; 29 Nov.–8 Dec. 2000; W. Villalba leg.; CNCI.

Description

Female

Measurements (n = 2). Head width (n = 1) 286; flagellomeres 29–33, 17–22, 23–24, 24–25, 26–29, 27–33, 30–33, 33, 45–50, 44–46, 49–51, 41–55, 64–69; AR 1.11–1.12; FR (n = 1) 1.62; wing length 1157–1200; wing width 414–444; costal ratio 0.56–0.57; spermathecal length 56–66; spermathecal width 56–57; spermathecal neck 17–18; spermatheca/neck ratio 0.3–0.32.

Thorax. Legs with femora and tibiae yellow.

Genitalia (Fig. 12d). 9th sternite anterior branch subacute, apices rounded, widely separated; posterior branch base directed anteriorly, apical half curving posteromedially, tip subacute. 2 major spermathecae.

Distribution

Magdalena, Vichada (Colombia) (Fig. 13).

Remarks

This provisional species may be conspecific with *C. virginianus*, as there are no morphological characters which separate them in the female stage. I have refrained from assigning these specimens to that species

until the male life stage for the Colombian material is collected. This species can be differentiated from all other species besides *C. virginianus* by the spermathecal length being <70 μm and concave medial margin of the 9th sternite having the posterior branch straight basally, tapering and curving only in its distal portion (Fig. 12d).

Ceratoculicoides sp. F2
Figs 6b, 12e

Diagnosis

Male
Currently unknown.

Female
Only species of *Ceratoculicoides* with the following combination of characters: femora brown, tibiae yellow, wing length ~0.9–1.1 mm; 2 major spermathecae, largest 70–75; medial margin of 9th sternite deeply concave.

Material examined

COLOMBIA • 1 ♀; Magdalena, Sierra Nevada de Santa Marta National Park, El Ramo; 10.8° N, 73.65° W; 15 Oct.–1 Nov. 2000; J. Cantillo leg.; CNCI • 1 ♀; Vichada, PNN Tuparro, Bosque Sabana; 5.35° N, 67.85° W; 29 Nov.–8 Dec. 2000; W. Villalba leg.; CNCI.

Description

Female
Measurements (n = 2): Head width 265–284; flagellomeres 25–31, 16–18, 19–22, 22, 23, 26–27, 26–31, 26–32, 36–40, 42–47, 45–46, 42–47, 49–53; AR 1.13–1.17; FR 1.5–1.55; wing length 947–1043; wing width 368–388; costal ratio 0.57–0.58; spermathecal length 70–75; spermathecal width 65–72; spermathecal neck 14–16; spermatheca/neck ratio 0.2–0.21.

Thorax. Legs with femora brown, tibiae yellow.

Genitalia (Fig. 12e). 9th sternite anterior branch apex broadly rounded, touching medially; posterior branch rounded, nearly as wide as anterior branch, tip not tapering, rounded. 2 major spermathecae.

Distribution

Magdalena, Vichada (Colombia) (Fig. 13).

Remarks

Major spermathecae with a length between 70 and 80 μm are found only in this species and *C. aliciae*. *Ceratoculicoides* sp. F2 differs from that species in the posterior branch of the 9th sternite being obtusely rounded (Fig. 12e), vs acutely pointed in *C. aliciae* (Fig. 11a).

Ceratoculicoides sp. F3
Fig. 12f

Diagnosis

Male
Currently unknown.

Female

Only species of *Ceratoculicoides* with the following combination of characters: femora and tibiae brown, wing length ~1 mm; 2 major spermathecae, largest 50–55; medial margin of 9th sternite deeply concave.

Material examined

COSTA RICA • 1 ♀; Puntarenas, Osa Peninsula, 4 km NW of Rincon; 11 Aug. 2001; A. Borkent leg.; CNCI • 1 ♀; same collection data as for preceding; Rio Agujas; 10–20 Aug. 1996; A. Azofeifa leg.; Malaise trap; CNCI.

Description

Female

Measurements (n = 2). Head width 256–306; flagellomeres 31–34, 21, 23–24, 23, 26, 24–26, 27–28, 29–31, 42–44, 46, 47–50, 43–51, 58–62; AR 1.14–1.21; FR 1.5–1.75; wing length 946–1016; wing width 371–397; costal ratio 0.63; spermathecal length 50–55; spermathecal width 46–56; spermathecal neck 8–11; spermatheca/neck ratio 0.16–0.2.

Thorax. Legs with femora and tibiae brown.

Genitalia (Fig. 12f). 9th sternite anterior branch apex broadly rounded, apices nearly touching medially; posterior branch acutely tapering at base, basal half directed posteriorly, apical half curving posteromedially, apex with small hook. 2 major spermathecae.

Distribution

Puntarenas (Costa Rica) (Fig. 13).

Remarks

Ceratoculicoides sp. F3 can be distinguished from other *Ceratoculicoides* by the combination of major spermathecae being <70µm, concave posterior margin of the 9th sternite with the posterior branch tapering in the basal half and ending in an acute point (Fig. 12f), and its flagellum ratio being >1.5. *Ceratoculicoides borkenti* sp. nov. is very similar, but its flagellum ratio is <1.5.

Unassociated Ceratoculicoides female specimens

Material examined

CANADA • 1 ♀; British Columbia, 23 km NW of Port Renfrew, Upper Carmanah Valley; 21 Jun.–3 Jul. 1991; N. Winchester leg.; CNCI • 4 ♀♀; same collection data as for preceding; 4–15 Jul. 1991; CNCI • 2 ♀♀; same collection data as for preceding; 31 Jul.–11 Aug. 1991; CNCI.

USA • 1 ♀; Arizona, Yavapai Co., Montezuma Castle National Monument, Montezuma Well; 15–16 Jun. 1987; M.W. Sanderson leg.; FSCA • 1 ♀; California, Imperial Co., Niland, Fountain of Youth Spa and RV Park; 22–27 Mar. 1982; J.R. Elmo leg.; light trap near mud from saline thermal springs; FSCA • 1 ♀; California; Riverside Co., Philip L. Boyd Deep Canyon Desert Research Center, S. Palm Desert; 23 May 1979; S. Frommer leg.; beating fronds of *Washingtonia*; FSCA • 1 ♀; Idaho, Idaho Co., Clearwater National Forest, Imnamatnoon Creek; 46.5149° N, 114.7635° W; 21 May 2017; A. Fasbender leg.; AFPC • 1 ♀; Montana, Missoula Co.,Lolo National Forest, Howard Creek above ponds; 46.7746° N, 114.5412° W; 4 Jul. 2018; A. Fasbender leg.; AFPC.

Phylogeny

The morphological phylogenetic analysis recovered one optimal tree with a score of 22 steps, presented in Fig. 14.

Discussion

Female characters and associations

The taxonomy of *Ceratoculicoides* has been complicated by the selection of *Helea longipennis* Wirth, 1952 as the type species, since the holotype of that species is a female and the paratype a second non-conspecific female. Neither of these types can be associated with a male morphospecies based on current evidence, especially as there are four *Ceratoculicoides* male morphospecies known from California, two of which have no female associations. The females of this genus are difficult to differentiate at the species level, with many characters used in other ceratopogonids being uniform or unreliable. The extent of spermathecal neck sclerotization is variable between otherwise identical specimens of a female series, suggesting it is not reliable to distinguish between species. I have discounted the use of a spermathecal ratio (length/width of spermathecae) as the width of the spermatheca varies depending on its orientation, and spermathecae are often collapsed and distorted during the clearing and slide mounting process. The chaetotaxy of the thorax also varies, especially the number of anepisternal and katepisternal setae. This is corroborated as intraspecific variability since conspecific males from the same site often have differing numbers of setae in the same positions. In contrast, the antennae, palpi and legs have proven largely identical throughout the genus.

I have found only four characters that potentially discriminate female morphospecies: flagellum ratio (FR), wing length, spermathecal length and the shape of the 9th sternites's genital sclerotization. The flagellum ratio (the length of the antennal flagellum divided by the width of the head) can be quite variable within a species, possibly related to allometric changes related to environmental conditions like those reported in the Chironomidae (McKie & Cranston 2005). This seems to be corroborated by *C. confusus* and *C. virginianus*, whose ranges cover a wide climatic gradient from eastern Canada to Florida and have markedly variable antennal and flagellar ratios. A smaller FR separates *C. borkenti* sp. nov. females from those of *C. virginianus*, *C.* sp. F1 and *C.* sp. F3, though this is based on a very small sample of material. Wing length divides the females of this genus into two groups, those with wings >1.5 mm (*C. longipennis* and *C. pacificus*) and the remainder of the species (whose wing lengths fall between 0.9 and 1.5 mm). There is some intraspecific variation in wing length, with for example *C. pacificus* female wings falling between 1.5 and 1.8 mm or *C. virginianus* wings measuring between 0.9 and 1.3 mm. Spermathecal length differs in three general ranges, with those >80 μm (*C. confusus*, *C. moravicus* and *C. pacificus*), those 70–80 μm (*C. aliciae* and *C.* sp. F2) and the remaining species with spermathecae <70 μm. Finally, the shape of the 9th sternite varies in the thickness and curvature of the dorsal and anterior branches (Figs 11–12). While the configuration found in *C. grogani* sp. nov. (Fig. 11e) is unique and recognizable due to its reduction of the posterior branch, examination of collection series for females confidently associated with the other species reveals there is significant variation in the thickness of both branches (ex Figs 11c–d, 12a–b) and even the curvature of these branches may not be diagnostic. The apparent separation between the medial apices of the sternite also appears to be influenced by the method of preparation and amount of compression that occurs during slide mounting. For these reasons, the key I have presented for the females of the genus should be viewed circumspectly, as I had access to very limited numbers of individuals for several species and some of the characters used may not be diagnostic upon comparison with a broader sampling of material. I have also avoided naming several unassociated female specimens, though some undoubtebly represent new species, and instead give them provisional designations. Without a male association such names would certainly result in future taxonomic confusion and instability, such as seen with ongoing ambiguity regarding the identity of *C. longipennis*.

Associating male and female specimens in *Ceratoculicoides* has proven challenging. Of the informative characters only wing length (a correlate of general body size) is of any use in associations, and this is even quite tenuous. I have been forced to rely heavily on series with a single morphotype of males

and females collected at the same locality (the syntopic method sensu Hogue & Bedoya-Ortiz 1989), which is not completely reliable. Future studies with additional material are badly needed to clarify the characters for distinguishing females and may challenge the associations inferred herein. Molecular barcoding holds promise for solidifying the female taxonomy of *Ceratoculicoides*, as it has proven extremely useful in associating life stages in other groups (e.g., Stur & Ekrem 2011).

Morphological character set

1. Setae on posterior margin of anterior anepisternum: (0), absent; (1), present (Fig. 3)
2. Dorsocentral punctations on scutum of female: (0), absent; (1) present
3. Sternite 9 of female: (0), pointed or rounded; (1), C-shaped (Figs 11–12)
4. Number of major spermathecae: (0), 2; (1), 1
5. Length of largest spermatheca: (0), <80μm; (1)>80 μm
6. Lateral margins of aedeagus: (0), convex (Fig. 8c, f, i); (1), straight or concave (Figs 9f, i, 10h, k)
7. Posterior margin of aedeagus: (0), convex (Fig. 8c, f, i); (1), straight or concave (Figs 9f, i, 10h, k)
8. Posteromedial hyaline incision of aedeagus: (0), absent (Fig. 8c, f); (1), present (Figs 8i, 9f, i)
9. Posterolateral point of aedeagus: (0), absent; (1), dorsally directed (at base) (Fig. 8c, f); (2), directed laterally (at base) (Figs 9f, i, 10h, k)
10. Apex of posterolateral point of aedeagus: (0), spiniform (Fig. 9i); (1), rounded (Fig. 10h, k)
11. Apical point of aedeagus: (0), absent (Fig. 8c, f); (1), separate from posterolateral point (if present) (Fig. 8i); (2), adjacent to or contiguous with posterolateral point (Figs 9c, f, i, 10h, k)
12. Accessory point present between apical and posterolateral points: (0), absent (Figs 9f, i, 10k); (1), present (Fig. 10c, h)

Phylogeny

Though the phylogenetic structure of the Ceratopogonini is poorly resolved (Borkent 2014), Borkent (1995) placed *Ceratoculicoides* in a clade consisting of *Brachypogon*, *Nannohelea* Grogan & Wirth, 1980, *Rhynchohelea* Wirth & Blanton, 1970 and *Sinhalohelea* Grogan & Borkent, 1992 based on the presence of synapomorphies consisting of setae on the katepisternum, with fusion of at least some of the male flagellomeres additionally uniting all these genera except *Sinhalohelea*. In describing *Ceratoculicoides*, Wirth & Ratanaworabhan (1971) noted the distinctiveness of the C-shaped sternite 9, suggested by A. Borkent as a synapomorphy of the genus (pers. comm.). Borkent (1992) proposed the presence of setae on the posterior margin of their anepisternum as another synapomorphy, noting it was unique within the Ceratopogonini. While some Palpomyiini and "Sphaeromyiini" s.l. (Borkent 2014) have setae on their anepisternum, they are more broadly distributed on the sclerite, indicating these are not homologous (Borkent 1992). Delécolle & Schiegg (1998) observed the presence of unique dorsocentral punctations on the posterior portion of the scutum in female *Ceratoculicoides*, which A. Borkent (pers. comm.) has hypothesized represents a third synapomorphy of the genus because it is unique in the Culicomorpha. The function of the punctations is unknown, though they may represent sensilla or pores (this merits histological study). The presence/absence and configuration of dorsocentral punctations in the males may have some phylogenetic signal, but this character has been difficult to interpret on slide mounted specimens (for some species, I had only one or two individuals to examine and typical lateral thoracic mounts obscure some of the dorsal surface of the scutum); thus, it was not included in this analysis. The morphological phylogeny produced in this study recovered a monophyletic *Ceratoculicoides* supported by four unambiguous synapomorphies: the aforementioned anepisternal setae (1;1), dorsocentral punctations on the scutum of the female (2;1), C-shaped sternite 9 of the female genitalia (3;1) and the presence of posterolateral points of the aedeagus (9;1,2), a feature noted by Wirth & Grogan (1988).

Interspecific relationships within *Ceratoculicoides* are well resolved. The best supported of these clades was a polytomy consisting of *C. borkenti* sp. nov. + *C. grogani* sp. nov. + (*C. aliciae* + *C. propinquus* sp. nov.+ (*C.* sp. M1 + *C. moravicus*)) , hereafter referred to as the "*C. moravicus* group". These

species are united primarily by possessing concave or straight lateral margins of the aedeagus (6;1), though this character state is shared with *Brachypogon* sp. L. I interpret this similarity to *Brachpogon* sp. L to be independently derived, as the other two outgroups have convex lateral margins and the *C. moravicus* group nests well within *Ceratoculicoides*, whereas all other species (including its sister taxa) have convex margins. Within the *C. moravicus* group, *C.* sp. M1 and *C. moravicus* are recovered as sister species based on the synapomorphic presence of accessory points between the apical and posterolateral points of the aedeagus (12;1); these species are included in a polytomy with *C. aliciae* and *C. propinquus* based on the synapomorphy of a rounded posterolateral point (10;1). The structure of all four species' male genitalia is extremely similar, differing only in the aforementioned accessory spines, the apical narrowing of the aedeagus in *C. aliciae* and *C. moravicus* and the presence of an acute apical notch along the posterior aedeagal margin in *C. aliciae*. The lack of narrowing towards the apex of the aedeagus in *C. propinquus* and *C.* sp. M1 may be a result of compression and distortion of the genitalia during slide mounting; see the taxonomic note for *C.* sp. M1 above regarding potential synonymy of that species with *C. moravicus*. *Ceratoculicoides tontoeguri* is supported as sister to the *C. moravicus* group based on the unambiguous synapomorphy of the posterolateral points of the aedeagus being directed laterally (9;2). Aditionally, the presence of a hyaline incision at the medial apex of the aedeagus (8;1) is shared between the *C. moravicus* group + *C. tontoeguri*, *C. pacificus* and *Brachypogon* sp. L, demonstrating the need for further outgroup comparisons. *C. virginianus* is weakly supported as sister to the C. *moravicus* group + *C. tontoeguri* by the straight or concave posterior margin of the aedeagus (7;1, also found in *Brachypogon* sp. L) and contiguous apical and posterolateral points (11;2). The final clade recovered was a sister group relationship between *C. confusus* and *C. pacificus*, based solely on the major spermathecae length >80μm (5;1). This is the same character that led Wirth & Ratanaworabhan (1971) to incorrectly associate the male of *C. confusus* with *C. longipennis* (see taxonomic notes for those species). A large spermatheca is also found in *C. moravicus* and *C. tontoeguri*, meaning this character state has independently arisen at least twice, therefore weakening its strength as a synapomorphy. In addition, a distinctively large spermatheca is present in numbers of other genera of Ceratopogonidae, suggesting this feature is susceptible to homoplasy.

The ground plan of several characters can be interpreted based on their distribution in the present phylogeny. Most *Ceratoculicoides* have two major spermathecae (4;0), including *C. tontoeguri* (Delécolle & Schiegg 1998, contra Havelka 1980), but *C. moravicus* has a single major spermatheca (4;1). Though *Brachypogon canadensis* also has a single major spermatheca, the other outgroup taxa combined with the distribution of this character within *Ceratoculicoides* indicates that two major spermathecae are the ground plan for the genus. Convex lateral (6;0) and posterior (7;0) margins of the aedeagus are another feature of the ground plan, being found in *S. gansi* and *B. canadensis*, though *Brachypogon* sp. L has the derived character state. Character 9, the posterolateral point of the aedeagus, can be separated into a type that emerges from the dorsal surface of the aedeagus (9;1) and another that emerges from the subapical lateral margin of the aedeagus (9;2). As the latter is a synapomorphy for the *C. virginianus* + *C. moravicus* group clade, the former state appears to be a symplesiomorphy within *Ceratoculicoides*. All *Ceratoculicoides* except *C.* sp. M1, *C. aliciae*, *C. moravicus*, *C. propinquus* sp. nov. and *C.* sp. M1 have a spiniform posterolateral point (10;0), another symplesiomorphy within the genus. The presence of apical points of the aedeagus appears to be part of the ground plan of *Ceratoculicoides*, as they are found in all species except *C. confusus*. In *C. pacificus* these points are well separated from the posterolateral points (11;1), but in the *C. moravicus* group and *C. virginianus* these points are adjacent and partially fused, typically with a concave arc forming their separation (11:2); it is unclear which of these character states is apomorphic. *Brachypogon* sp. L has similar apical points at the median apex of the aedeagus, and it is currently uncertain whether these are homologous with those in *Ceratoculicoides*.

Since *Brachypogon* sp. L shares several character states with certain *Ceratoculicoides*, the morphological dataset was reanalyzed with that taxon removed. The same ingroup tree topology was recovered, though the Bremer support values for the branch supporting *Ceratoculicoides* improved to four. *Brachypogon* is extremely speciose and varied in morphology, and an understanding of the diversity and phylogeny of that genus will be critical to interpreting the evolution of related genera. Similarly, comparison of material of *Nannohelea* and *Rhynchohelea* should also improve our comprehension of the relationships within *Ceratoculicoides*.

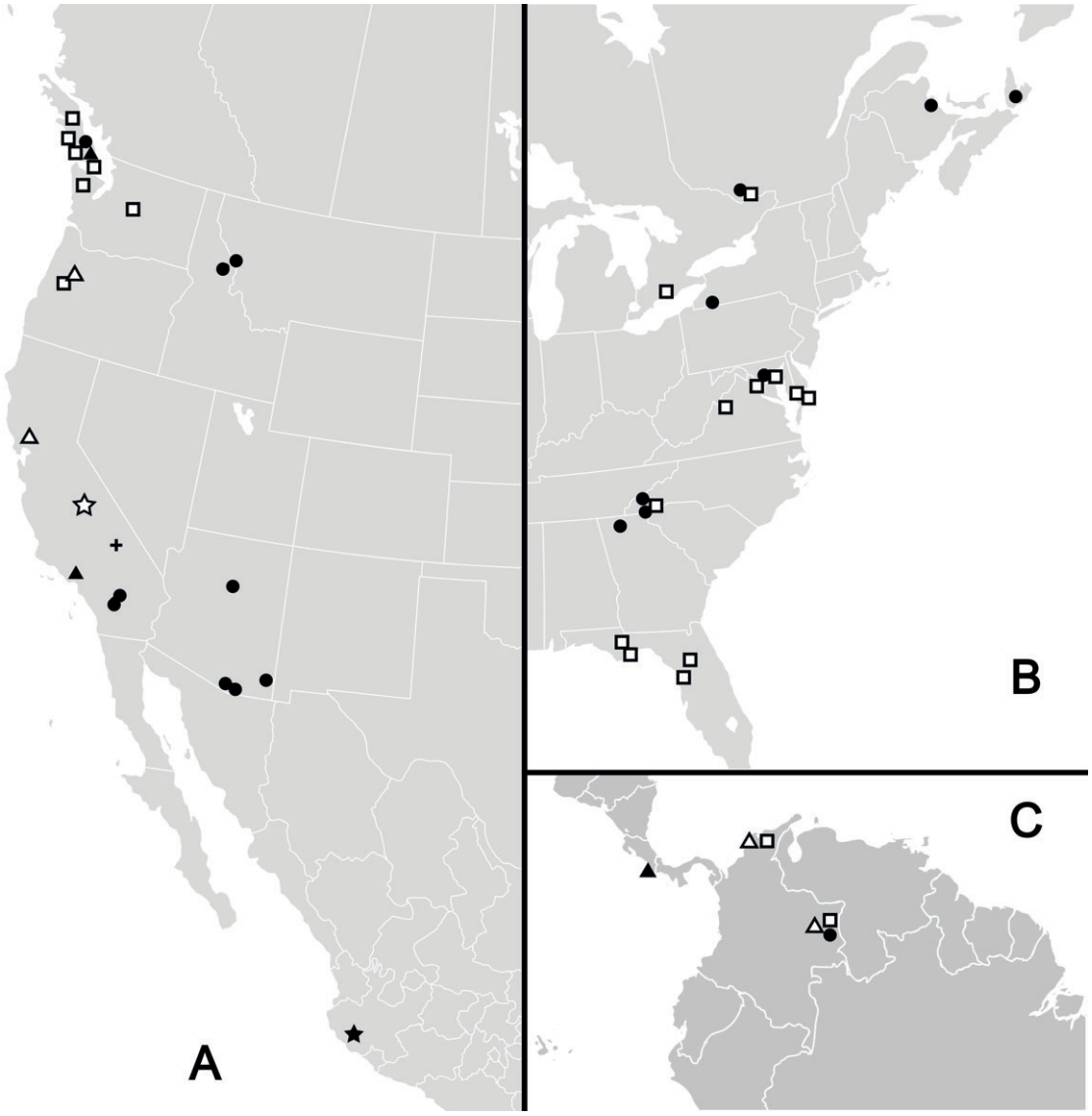

Fig. 13. Distribution. **a**. Western North America. Solid star = *Ceratoculicoides aliciae* Huerta & Borkent, 2005; solid circles = *C. borkenti* sp. nov.; open triangles = *C. grogani* sp. nov.; open star = *C. longipennis* (Wirth, 1952); open square = *C. pacificus* sp. nov.; solid triangle = *C. propinquus* sp. nov.; solid cross *C.* sp. M1. **b**. Eastern North America. Solid circles = *C. confusus* sp. nov.; open squares = *C. virginianus* (Wirth, 1951). **c**. Central and northern South America. Solid circle = *C. confusus*; open squares = *C.* sp. F1; open triangles = *C.* sp. F2; solid triangle = *C.* sp. F3.

There is a single fossil species referred to *Ceratoculicoides* from ~50 mya Baltic amber, *Ceratoculicoides danicus* Szadziewski, 1988. Known only from females, it has the combination of raptorial fore and midleg tarsal claws with small claws on the hindleg that characterize the genus but differs in a number of features from extant species of *Ceratoculicoides*. These include fourth and fifth segments of the maxillary palpus fused (vs separate), strongly unequal tarsal claws (vs equal or slightly unequal), and a large r_2 cell (vs reduced or absent) (Szadziewski 1988). The presence of anepisternal setae, dorsocentral punctations on the scutum or the structure of the 8th sternite are not noted in the original description, making this species placement in *Ceratoculicoides* somewhat challenging to assess. Absent additional evidence, I suggest retaining *C. danicus* in *Ceratoculicoides* based on the tarsal claw character, though it does not conform to several other features of the extant fauna.

Bionomics and distribution

The natural history and ecology of *Ceratoculicoides* remains poorly understood. I have personally collected only *C. borkenti* and some unassociated females from a handful of sites in the Bitterroot Mountains near the Idaho-Montana border (USA). Each instance was near water: once along a series of beaver ponds, twice along streams approximately 6–10 m wide with shallow side channels. All specimens were collected by sweeping riparian vegetation, though specific adult microhabitats were not noted, as *Ceratoculicoides* cannot be reliably differentiated in the field without microscopy. Each incident resulted in only a single specimen collected, and most of the other material I have examined also consists of a handful of specimens from an individual collection event. An exception is several large series of *C. pacificus* that were collected by Neville Winchester in the temperate rainforest of Vancouver Island (Canada). The relatively coarse mandibular teeth and elongate, raptorial tarsal claws on the fore and midlegs of adult female *Ceratoculicoides* suggest they are aerial predators of small flying insects like many other members of Ceratopogonini (Borkent 1995). The immature stages and larval microhabitat remain unknown, as is the case for over half of the genera in Ceratopogonidae (Borkent 2014).

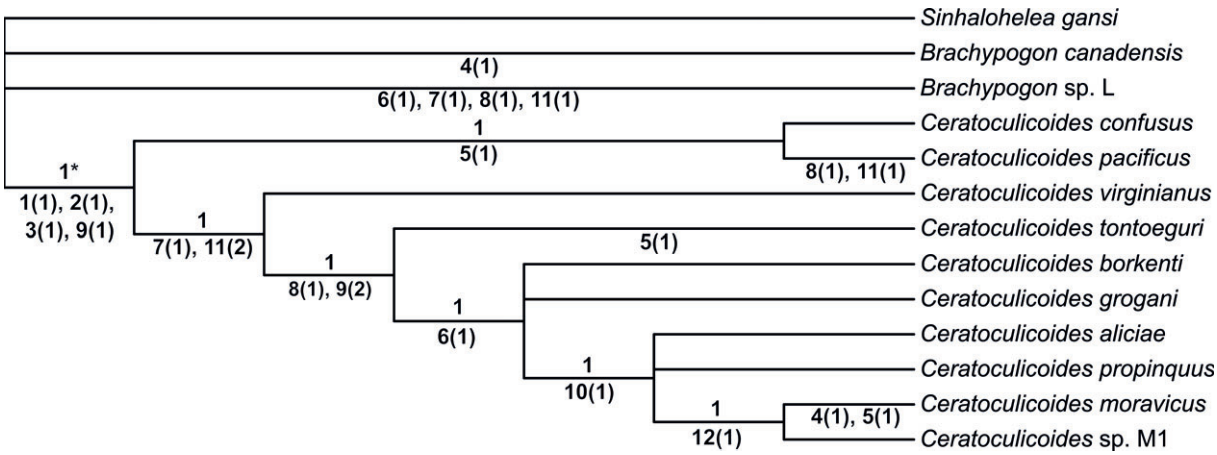

Fig. 14. Morphological phylogeny (Maximum Parsimony) of *Ceratoculicoides* Wirth & Ratanaworabhan, 1971 (unsupported branches collapsed). Bremer support values are noted above and character state changes (given as character # (state)) below branches. * Bremer support value increased to 4 in a reanalysis removing *Brachypogon* sp. L from dataset (see Discussion).

Our current understanding of Nearctic species distributions must be considered preliminary, with several species (*C. grogani* sp. nov., *C. longipennis*, *C. propinquus* sp. nov. and *C.* sp. M1) known only from one or two localities, and two species (*C. propinquus* and *C. confusus*) with disjunctions of over 1200 km between populations. *Ceratoculicoides borkenti*, though known from more specimens and localities, exemplifies the patchy distribution of records within the genus. That species has been recorded from three distict ecoregions: the Desert Southwest of Arizona and California, the Northern Rocky Mountains of Idaho and Montana and the temperate rainforest of Vancouver Island. Separating these clusters are swathes of apparently suitable habitat spanning 700–1300 km, suggesting additional populations of *C. borkenti* sp. nov. await discovery. As the species fauna of the eastern and western Nearctic is disjunct for the genus, sampling in the center of the continent is of interest to establish the range limits of existing taxa and may uncover additional undescribed species. There are near total gaps in records for the genus across the Great Basin, Middle Rocky Mountains, Great Plains, Prairie Peninsula, Ozarks, and the Gulf Coast.

Our knowledge of *Ceratoculicoides* in the Neotropics remains extremely preliminary. For example, *C. aliciae* remains known only from the type series, while males have not been located for female material from Costa Rica (Huerta & Borkent 2005; Borkent *et al.* 2009) and whether it represents a distinct species remains obscure. The discovery of a *C. confusus* male in Colombia expands the range of the genus into the northern part of South America, where there is a paucity of knowledge on the ceratopogonid fauna (Borkent *et al.* 2018). Two females have been collected from a high elevation (> 4000 m) at the Páramo site within Sierra Nevada de Santa Marta National Park in northeast Colombia, though like the Costa Rican material, there are no associated males to illuminate their identity. Further sampling in Central and South America will undoubtably uncover additional populations and probably new species of *Ceratoculicoides*. As in the Nearctic, essentially nothing is known of the natural history of the Neotropical fauna for this genus. The report of female *Ceratoculicoides* specimens from North Korea by Szadziewski (1988) indicates that there is also an Asian fauna that remains totally unexamined.

Conclusion

The New World fauna of *Ceratoculicoides* has been expanded from four named species to eight, with five new species (*C. borkenti* sp. nov., *C. confusus* sp. nov., *C. grogani* sp. nov., *C. pacificus* sp. nov. and *C. propinquus* sp. nov.). *Ceratoculicoides confusus* represents the first record of the genus from South America. *Ceratoculicoides blantoni* was synonymized with *C. virginianus* due to the original characters separating the species not proving to be diagnostic based on the examination of a broad range of material. Phylogenetic analysis supports the monophyly of the genus and the recognition of the *C. moravicus* species group. The natural history of the genus remains obscure, with the immature stages unknown and adult habits speculatively inferred.

Acknowledgments

Art Borkent initiated this revision when I approached him about a specimen of *Ceratoculicoides* I had collected in Idaho, generously offering the specimens, literature and unpublished observations he had gathered for his own study of the genus. Bill Grogan provided more material and corroborated my views on the difficulties in separating the females of this group. Scott Brooks (CNCI), Torsten Dikow (USNM), Bill Grogan (FSCA), David Pecor (USNM), Brad Sinclair (CNCI) and Gary Steck (FSCA) facilitated loans. Travel to examine the USNM material was enabled by a grant from the S.W. Williston Diptera Research Fund. Art Borkent, Bill Grogan, Barbara Hayford, Jeff Webb and an anonymous reviewer provided comments that improved earlier versions of this manuscript.

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