CHIRONOMUS Journal of Chironomidae Research No. 40, 2025: 73-90. Special Issue LCF Memorial.

DESCRIPTION OF *PARAKIEFFERIELLA FERRINGTONI* WITH DISCUSSION OF RELATIONSHIPS WITHIN THE *PARAKIEFFERIELLA* GROUP (DIPTERA, CHIRONOMIDAE, ORTHOCLADIINAE)

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Abstract

Parakiefferiella ferringtoni sp. n., previously recorded as the provisional taxon Orthocladiinae Genus 5 *sensu* Coffman and Ferrington (2008), is described based on larval, pupal, pharate male and female material. This species resides in the Pacific Northwest region of the Nearctic. The morphology of *P. ferringtoni* sp. n. blurs the lines between genera of the *Parakiefferiella* group. We review the state of generic taxonomy of the *Parakiefferiella* group, with an emphasis on providing explicit morphological synapomorphies to delineate each genus, although *Parakiefferiella* Thienemann and *Lappokiefferiella* Tuiskunen have no unambiguous synapomorphies.

Introduction

The Chironomidae fauna of the western Nearctic is poorly known, having only received a cursory survey in the literature (Sæther 1969, Sublette & Sublette 1971, Sublette et al. 1998, Namayandeh & Culp 2016). Despite the paucity of published taxonomic studies, there is a network of organizations conducting aquatic bioassessment in western North America, including federal, state, local and tribal entities (Roper et al. 2010). Immature Chironomidae are an integral part of these programs, typically identified to genus, though a few taxa are taken to species or species group. In addition to established taxa there are also morphotypes which do not conform to current genus concepts (Fasbender 2020).

This study is based on long-term chironomid data generated via collaborations of Rhithron Associates, Inc. (RAI) with state, county, city, and other entities assessing freshwater systems. RAI maintains an internal catalog of provisional taxa designations for morphotypes not conforming to established genera to provide consistent reporting of these taxa. With client permission we also retain unusual specimens from samples, typically larvae and pupae as these are benthic samples. One such taxon found in the Pacific Northwest is Orthocladiinae Genus 5, a provisional taxon previously known only in the pupal stage (Coffman and Ferrington 1996, Ferrington et al. 2008, Ferrington and Berg 2019).

The pupa of Orthocladiinae Genus 5 is distinctive, similar to *Rheosmittia* Brundin, except it has an ovoid thoracic horn and lacks the flattened D5 setae that characterizes that genus. We were able to find associated material of the heretofore unknown larvae, which resemble *Parakiefferiella* Thienemann except for a very narrow median tooth subequal in size and aligned with the first lateral teeth of the mentum. Examination of pupae with pharate adults showed they are of the *Parakiefferiella* group type, but do not key out properly to that genus based on the diagnosis of Cranston et al. (1989). The adults fall into the *Parakiefferiella* group of genera with a curved gonostylus but do not have a medial setal tuft or tubercle on the scutum. Examining a range of material of this unusual taxon and attempting to place it into a genus led us to reexamine the characters used to delimit genera within the *Parakiefferiella* group. Although we did not have access to eclosed adult material, based on the characters of the immatures and the absence of a setal tuft or tubercle along diagnostic male genitalia there is sufficient justification to formally name this taxon (Fasbender 2020) and describe this species as *Parakiefferiella ferringtoni* sp. n.

The decision to place Orthocladiinae Genus 5 within *Parakiefferiella* lead us to examine relationships between *Parakiefferiella* and closely related genera, thereby broadening the scope of this research. The goals of our research are to:

Describe all three life stages of *P. ferringtoni* sp. n.

Suggest amendments to existing keys to include *P. ferringtoni* sp. n.

Update the species keys for Nearctic *Parakiefferiella* to include *P. ferringtoni* sp. n.

Briefly review taxa in the *Parakiefferiella* group (*sensu* Sæther 1983) and the characters that define them.

Methods and materials

The material used in this study originated from 2001-2021 bioassessment programs from the following organizations: the Cities of Bellevue, Bellingham, Bainbridge Island, Bothell, Federal Way, Issaquah, Kirkland, and Redmond; King County; Montana Department of Environmental Quality; Pierce County; Seattle Public Utilities; Snohomish County Public Utilities Division; Vashon Nature Center, LLC; and the Washington State Department of Ecology. Most of the specimens examined were retained by the originating entity, although select individuals have been deposited in the Academy of Natural Sciences of Drexel University [ANSP] or Andrew Fasbender's personal collection [AFPC]. All material examined was mounted on slides unless otherwise noted in the material examined.

Descriptive terminology follows Sæther (1980), except for the use of "ommatrichia" for the microtrichia between ommatidia of the adult eye, epandrium for the structure called "Tergite IX" in Sæther 1980, gonopod for the clasping structure consisting of the gonocoxite and gonostylus, genital fork for the structure called "Gonapophysis IX" in Sæther 1980 and spermathecae (Cumming and Wood 2017). The female description only contains those characters which differ from the male. All measurements are given in µm unless otherwise noted, the anal point was measured from the posterior apex to the anterior setae (as there is not a distinct separation of it from the remainder of the epandrium). Life stage associations were made using the ontogenetic method sensu Hogue and Bedoya Ortiz (1987). Specimens were cleared using Tergazyme© enzymatic detergent, transferred to 99% isopropanol, dissected, and mounted in Canada balsam on microscope slides. A Leica DM1000 compound microscope equipped with an Amscope MU1000 camera was used to examine specimens. The Amscope 4.11 software package was used to capture images and take calibrated measurements. Illustrations were rendered using Inkscape 1. Data were exported to Microsoft Excel to create a distribution map generated with SimpleMappr (Shorthouse 2010). Sites on the distribution map not included in the material examined come from the RAI database.

Our review of taxa and morphological characters in the *Parakiefferiella* group is based on examination by the senior author and characters in Sæther (1983), Coffman et al. (1986), Cranston et al. 1989 and Andersen et al. (2013).

Results

Parakiefferiella ferringtoni sp. n.

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Orthocladiinae Genus 5 (Ferrington et al. 2008, Ferrington and Berg 2019).

Possibly Orthocladiinae gen.? sp.? NA7 and *Parakiefferiella* NA3 (Langton 2023).

Orthocladiinae RAI #0011 (for larva).

Type material. Holotype male pupa (slide), USA, WASHINGTON, *King Co.*, Vashon Island, Shinglemill Creek, 47.4762°N, 122.4815°W, 13.ix.2021, KC21AMB02064 (ANSP-ENT-124842), on slide [ANSP]. Paratypes: 1 male (ANSP-ENT-124843), 2 female pupae (ANSP-ENT-124844, 124846), 1 larva (ANSP-ENT-124847) on slide as holotype [ANSP]; 1 male pupa, USA, MONTANA, *Beaverhead Co.*, Willow Creek at base of Thunderhead Mountain, 45.448°N, 112.8277°W, 15.vii.2019 (ANSP-ENT-124848) on slide [ANSP]; 7 larvae, WASHINGTON, *King Co.*, Cedar River Lower Tributary (0311), 47.4614°N, 122.1255°W, 25.viii.2016 08CED2898_16 KC16AMB2040, in vial [AFPC], 7 larvae as previous, 10.viii.2017 08CED2898_17, KC17AMB4038, in vial [AFPC]; 1 male pupa, High Point Creek, 47.5319°N, 121.9762°W, 1.viii.2018 08ISS4573_18, KC18AMB2018, (ANSP-ENT-124850) on slide [ANSP]; 1 male pupa, Holder Creek, 47.4339°N, 121.9719°W, 9.viii.2017, 08ISS4730_17, KC17AMB4035 (ANSP-ENT-124851, on slide [ANSP]); 3 larvae, Holder Creek, 47.5319°N, 121.9762°W, 1.vii.2018, 08ISS4573_18, in vial [AFPC]; 7 larvae, Vashon Island, Christenson Creek, 47.4027°N, 122.5169°W, 20.ix.2017 KC-17VAS001, in vial [AFPC]; 1 larva, *Kitsap Co.* Chico Creek, 24.viii.2011, in vial [AFPC]; 1 female pupa, Garst Creek, 29.viii.2011, in vial [AFPC]; 2 female pupae, 5 larvae, Little Anderson Creek 29.viii.2011, in vial [AFPC]; 1 male (ANSP-ENT-124852), 1 female pupa (ANSP-ENT-124854) *Pacific Co.*, Basin 7315, 46.3241°N, 123.7668°W, 26.iv.2016, WADOE16MM019, slide [ANSP]; 5 female pupae (2 with associated larval exuviae) as previous, in vial [AFPC]).

Etymology. This species is named in honor of Leonard "Len" Ferrington Jr., in recognition of his contributions to Nearctic chironomid studies and mentorship of the last author.

Diagnostic characters. *Adult male (pharate).* As per *Parakiefferiella* except scutum without medial tubercle or setal tuft, inferior volsella subquadrate, with anteromedial corner rounded, glabrous and expanded beyond medial margin. *Pupa.* Thoracic horn ovoid with scale-like spinules, tergites with band of dark triangular spinules posteriorly, anal lobes coming to an acute point, without setal fringe, macrosetae absent or if present minute (< 0.1 x length of anal lobe). *Larva.* SI plumose, mentum with single median tooth subequal in width and height to first laterals giving the appearance of three median teeth, ventromental plates not extending beyond lateral teeth, antenna with hair-like 6th segment.

Description. *Adult male (pharate).* Figs 1, 3a. Measurements (n = 3): Flagellomeres 17–31 (18), 15–20 (18), 16–20 (19), 28–29 (29), 34–45 (42), 37–42 (39), 39–42 (40), 38–42 (41), 34–44 (38), 35–40 (39), 34–39 (35), 32–38 (37), 128–203 (175); AR 0.33–0.50 (0.44); anal point 42–46 (44); virga 61–75 (63); gonocoxite 113–121(115); gonostylus 40–45 (43). Habitus pale.

Head. Verticals absent, 1 postorbital. Antenna with 13 flagellomeres, plume present. Eyes reniform. Clypeus ovoid but not inflated, tapering ventrally, with five setae on dorsal margin. Tentorium not visible on specimens examined. Maxillary palpus with five segments.

Thorax. Antepronotum not narrowed medially, setae absent. Acrostichals absent, 1 dorsocentral above scutellum, 3 uniserial prealars, single scutellar. Postnotum bare.

Wing. Veins without setae, venation otherwise not apparent.

Legs. Sensilla chaetica absent. Tibial spur formula 1-1-2. Pseudospurs absent. Pulvilli lanceolate, 2/3 length of tarsal claws.

Abdomen. Tergites II–V with three pairs of setae in arched row, middle pair set distinctly anterior to lateral pairs; tergites VII and VIII similar, but with first lateral pair of setae moved medially directly posterior to medial pair of setae; tergite VI variable, resembling either anterior or posterior tergites. Sternites I–IV without setae, V–VIII with irregularly spaced setae.

Hypopygium. 2–3 setae on each side of anal point. Lateral margins of gonocoxite straight; superior volsella low and rounded, inferior volsella protruding and squared off apically: anteromedial corner glabrous, rounded and slightly expanding beyond straight medial margin, posteromedial corner with brush of fine setae. Gonostylus curve starts at 2/3rd of the length, megaseta forked, with small tooth directly ventrally. Very small lentiform pars ventralis present. Sternapodeme trapezoidal, lateral apices of oral projections hooked, anterior apices

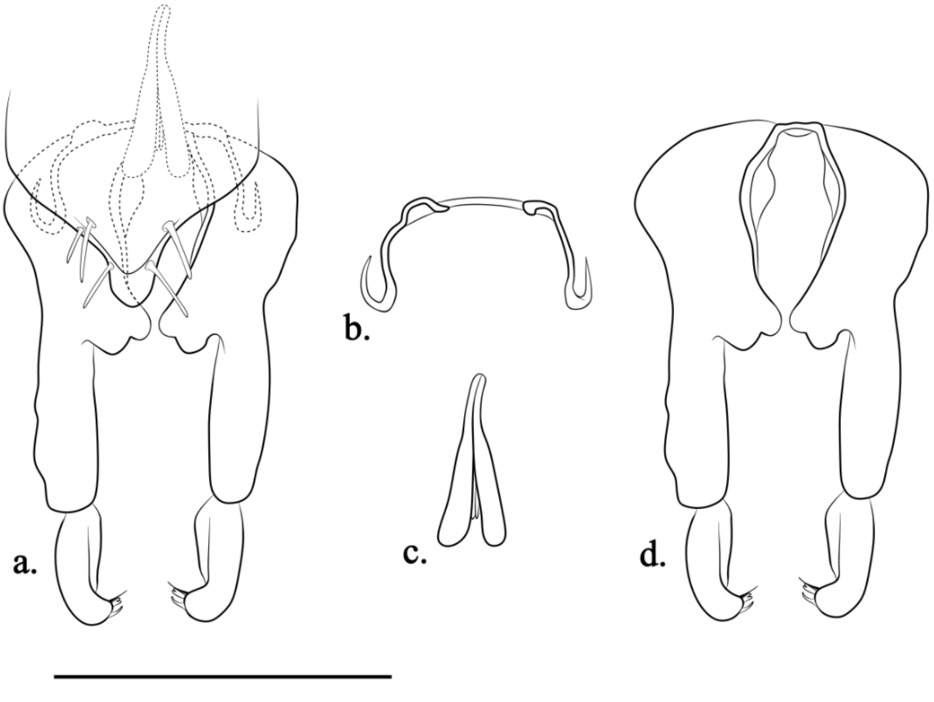

Figure 1. *Parakiefferiella ferringtoni* sp. n. male genitalia: a. dorsal view (overall), b. transverse sternapodeme, c. virga, d. gonopods, unobscured. Scale bar 100µm.

low and quadrate; phallapodemes inconspicuous. Virga with two flattened dorsal scales expanding posteriorly, curving in a C shape to an acute ventral terminus.

Adult female (*pharate*). Figs 2, 3b. Measurements (n = 3): Flagellomeres 21–44 (39), 33–42 (35), 31–42 (40), 33–41 (38), 76–138 (97); AR (n = 1) 0.6; cercus 58–78 (73) genital fork 125–150 (151), notum 83–97 (92), ramus 42– 54 (48); spermathecae (n = 2) 45–57 x 36–39, 46–58 x 32–43. Habitus pale.

Head. 1-2 postorbitals. Antenna with 5 flagellomeres, plume absent.

Genitalia. Tergite IX semicircular, with 6-10 setae, without projections or lobes. Gonapophysis VIII dorsomedial lobe rounded triangular, medial margins parallel and lined with setae; ventrolateral lobe rounded with brush of long setae on ventral surface. Apodeme lobes indistinct.

Pupa. Figs 4, 5b-d. Measurements: overall length (n = 5) 1.8–2.2 (2.0) mm; thoracic horn length (n

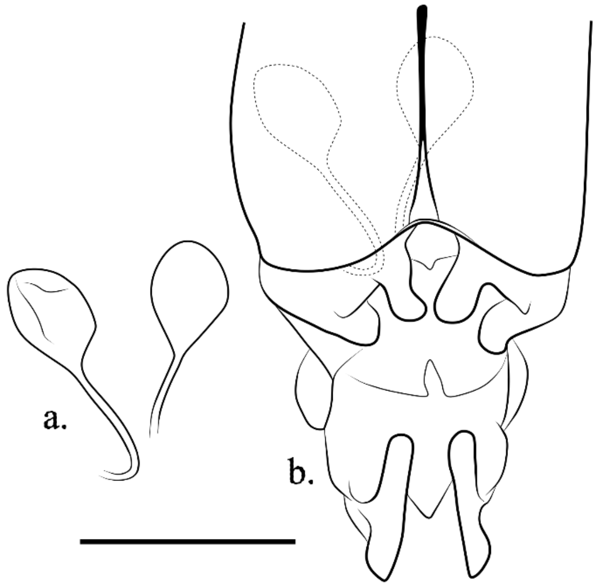

Figure 2. *Parakiefferiella ferringtoni* sp. n. female genitalia: a. spermathecae, b. ventral view (overall). Scale bar 100µm.

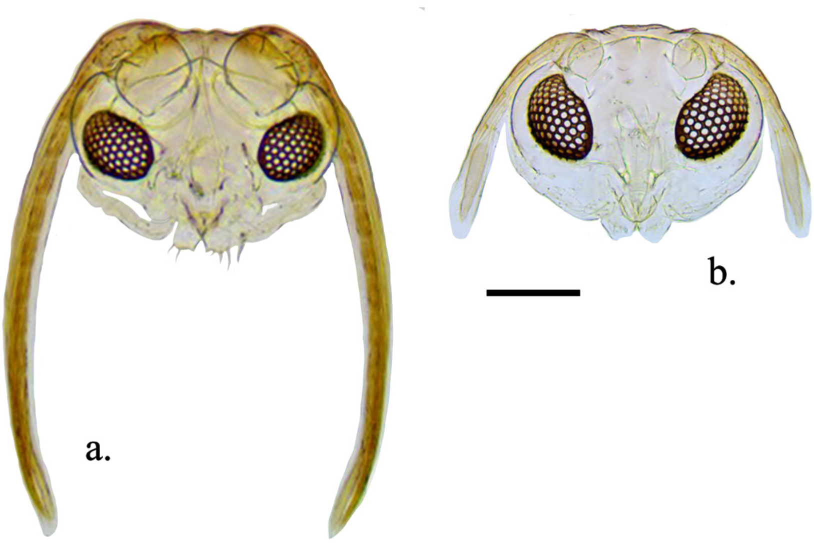

Figure 3. *Parakiefferiella ferringtoni* sp. n. adult heads: a. male, b. female. Scale bar 100µm.

= 3) 64–72 (66), anal lobe length (n = 3) 167–181 (171); female genital sac (n = 3) 76–114 (109); male genital sac (n = 3) 174–199 (183). Habitus pale.

Cephalothorax. Cephalic tubercles and frontal warts absent. Frontal setae absent. Antennal sheath smooth. Postorbitals absent. Antepronotum with one median and one lateral seta, both simple. Thoracic horn ovoid, 1.5x longer than broad, 70–80 μm; surface with scale-like texturing. 2–3 precorneals present, other thoracic setae absent. Anterodorsal surface of thorax rugose.

Abdomen. Tergites I and VII-VIII without shagreen, tergites II-VI with minute widely spaced triangular shagreen (Fig. 5d). Posterior margins of tergites II-VII with dark triangular spinules, conjunctives III and IV with medial patch of hyaline spines. Pedes spuria A and B absent. Sternites without shagreen or spinules. Abdominal setation: tergite I 5 D, 0 L, 4V; tergites II-VII 5D, 3L, 3V; VIII 3 D, 3L, 1V. No taeniae. Anal lobe without rounded lateral section narrowing to acute point curved dorsally, with irregular serrations scattered towards apex. No fringe present, macrosetae often absent. When present 0–3 minute macrosetae (< 0.1 x length of anal lobe) at 3/4th of the length of anal lobe, placed dorsolaterally. Male genital sac subequal in length to anal lobes, with apical papilla developed only as a slight tapering at apex; female genital sac trapezoidal, extending 1/3 anal lobe length.

Larva. Figs 5a, 6. Measurements (n = 11): overall length 2.7–3.2 (2.9) mm. Overall habitus pale, cranium light yellow.

Antenna. 6 flagellomeres, 1.3x length of mandible, antennal ratio 0.8. Ring organ not apparent on specimens examined. Blade reaching the apex of flagellomere 4. 2nd flagellomere weakly expanding

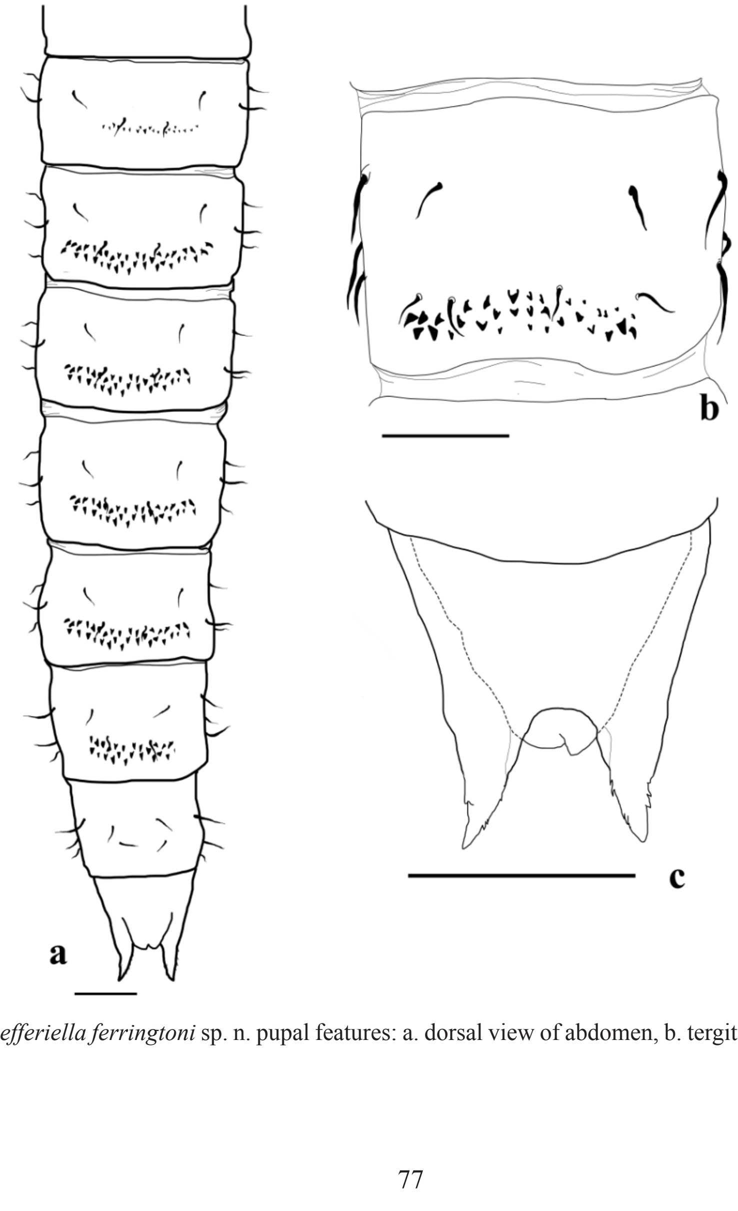

Figure 4. *Parakiefferiella ferringtoni* sp. n. pupal features: a. dorsal view of abdomen, b. tergite VII, c. anal lobes. Scale bars 100µm.

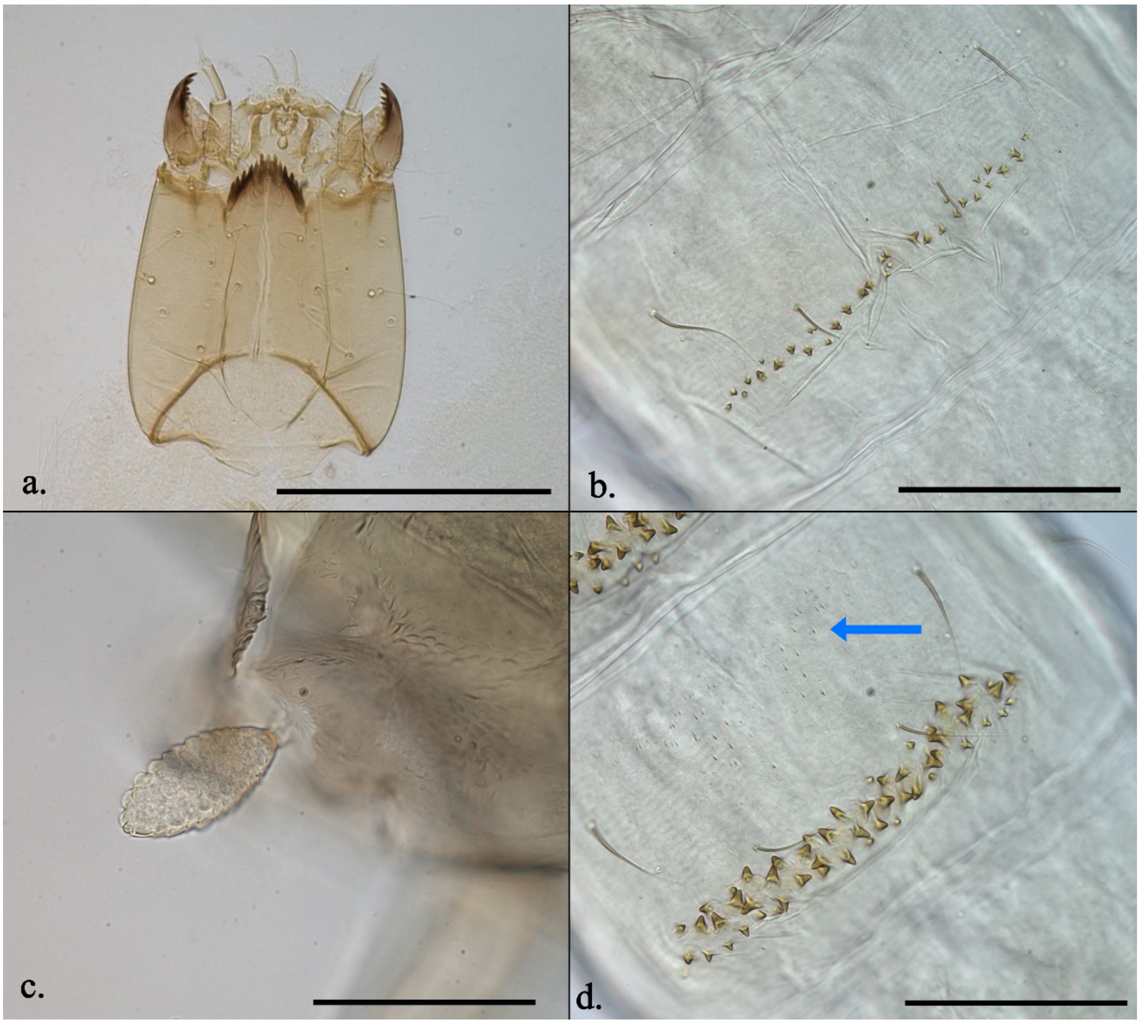

Figure 5. *Parakiefferiella ferringtoni* sp. n. photomicrographs: a. larval head capsule, b. pupal tergite II, c. pupal thoracic horn, d. pupal tergite IV, blue arrow indicates shagreen spinules. Scale bars 100µm.

towards apex. Lauterborn organs distinct, extending to apex of 3rd flagellomere. Flagellomeres 4 and 5 ~2x length of flagellomere 3, flagellomere 6 hairlike.

Labro-epipharyngeal region. SI broad, plumose. SII large, bladelike, other S setae reduced. Chaeta media reduced. Labral lamellae absent. Pecten epipharyngis with three, minute spines. Chaetulae laterales simple. Premandible with 2 apical teeth, 1 broad inner tooth dorsally; brush absent.

Mandible. With 3 teeth inner teeth, apical tooth ~0.3 length of inner teeth. Seta subdentalis with hooked apex, extending to first inner tooth; seta interna divided to base with numerous simple branches, difficult to discern, not extending beyond the margin of the mola.

Mentum. Triangular, with median tooth subequal in width and height to first laterals, creating a trifid appearance, projecting above five other pairs of lateral teeth. Ventromental plates narrow, paralleling lateral teeth, do not extend beyond them. Setae submenti placed further than halfway up the mentum, well anterior to ventromental plate apex. Beard absent. Hypopharyngeal scales absent.

Body. Anterior parapods separate, claws serrate. Posterior parapods 2.75–3x longer than wide, claws simple. Procerci length subequal to width, with 4–5 anal setae longer than posterior parapods. Supraanal setae shorter than posterior parapods. Anal tubules shorter than posterior parapods, apex pointed. Abdominal segments without prominent setae, cuticle appearing waxy.

Distribution. Pacific Northwest and Northern Rocky Mountains (Fig. 7).

Remarks. The pupa of *P. ferringtoni* was keyed as “Genus 5” in Coffman and Ferrington (1996), Ferrington et al. (2008) and Ferrington and Berg (2019). This species also keys to “Orthocladiinae

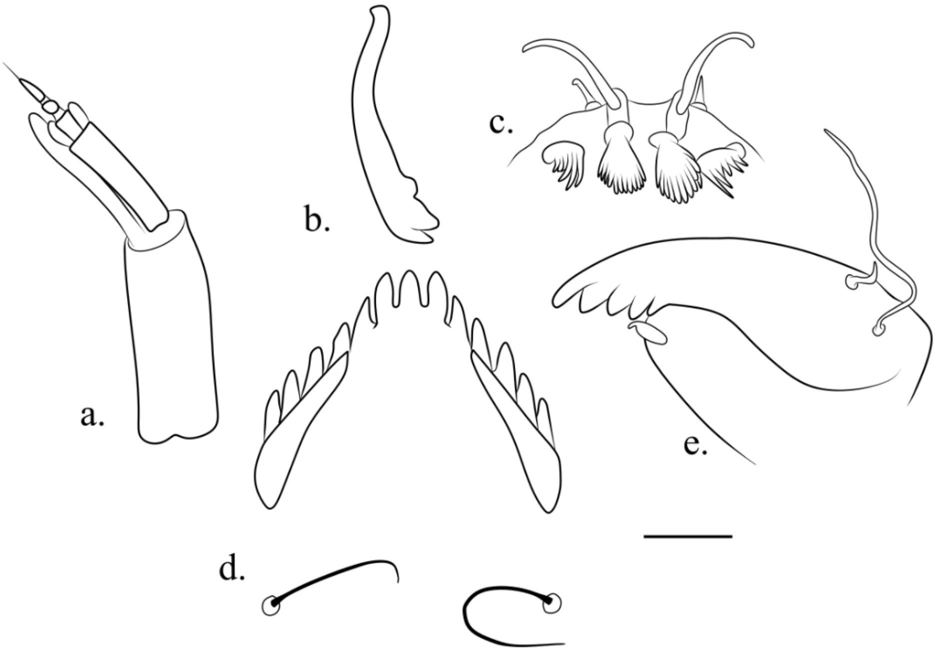

Figure 6. *Parakiefferiella ferringtoni* sp. n. larva: a. antenna, b. premandible, c. labral setae, d. mentum, e. mandible. Scale bar 100µm.

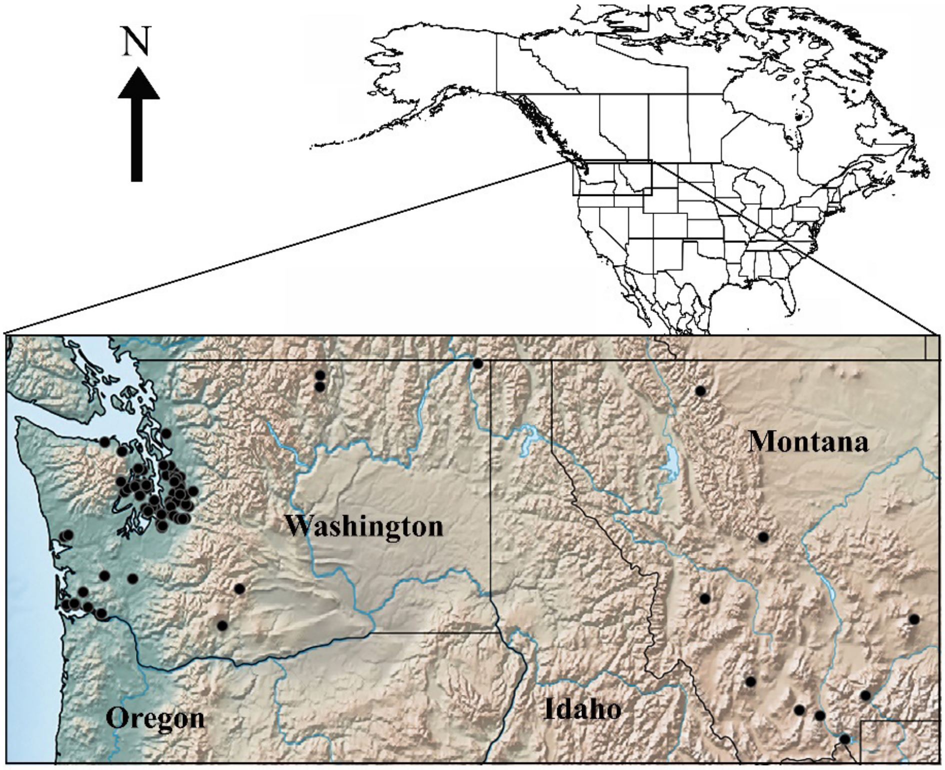

Figure 7. Distribution map of *Parakiefferiella ferringtoni* sp. n. examined for this study. Black circles indicate sampling localities for material examined.

gen.? sp.? NA7" in Langton (2023). However, the thoracic horn is not as tapering as illustrated for that provisional taxon. *Parakiefferiella ferringtoni* also has some similarities to *Parakiefferiella* NA3 in the same key, although the configuration of L setae appears slightly different and *P. ferringtoni* lacks a hook row on segment II. RAI has found associated larval specimens and pharate adults on which this description is based. *Parakiefferiella ferringtoni* is similar in the larval stage to other *Parakiefferiella* in having a hairlike 6th antennal flagellomere and to *Rheosmittia* (Cranston and Sæther 1986) in overall habitus, especially the conical head capsule, though it has significant differences from both genera. It differs primarily from other *Parakiefferiella* in the structure of the median tooth of the mentum. The median and first pair of lateral teeth are subequal in width and are of the same height in *P. ferringtoni* versus typical *Parakiefferiella* where the median tooth is wider than the first laterals and projects anterior to them. Additionally, the apical tooth of the mandible is subequal to or longer than the inner teeth in most *Parakiefferiella,* whereas it is subequal in size to the distal inner tooth in *P. ferringtoni. Rheosmittia* differs in the labral SI setae, which are simple in *Rheosmittia,* and plumose in *P. ferringtoni*. The hypopharyngeal scales of *Rheosmittia* are absent in *P. ferringtoni* and setae submenti reduced in *Rheosmittia* but normally developed in *P. ferringtoni*. *Rheosmittia* has a five segmented antenna with the second flagellomere divided by a desclerotized break, whereas the antenna is six segmented in *P. ferringtoni*.

While the three medial teeth of *P. ferringtoni* could be interpreted as a trifid median tooth, the presence of five other pairs of lateral teeth indicated the outer medial teeth are actually the first pair of laterals, as other species of *Parakiefferiella* have six pairs of lateral teeth. Thus the larva of *P. ferringtoni* correctly keys out to *Parakiefferiella* in couplet 72 of Andersen et al. (2013), provided the three subequal medial teeth of the mentum are correctly interpreted as a single median tooth and the first pair of lateral teeth. These three subequal teeth of uniform height are unique among *Parakiefferiella* larvae and readily allow the diagnosis of *P. ferringtoni* from the other species for which larvae are known. While there are some species in other genera with a similar configuration of three subequal teeth medially on the mentum (i.e. *Parorthocladius*, some *Cricotopus*), genus level characters readily distinguish them from *P. ferringtoni*.

The number of anal macrosetae is quite variable between pupal specimens, with many having no macrosetae while other individuals from the same locality have 1–3 minute macrosetae on the dorsolateral surface about 3/4 down the length of the anal lobe. We have even examined one specimen with two macrosetae on the left anal lobe and only one on the right. Setal sockets were not observed in pupal specimens lacking anal macrosetae, indicating this variability is not merely loss due to damage or wear.

The adult of *P. ferringtoni* keys out to the genus *Krenosmittia* based on Cranston et al. (1989) couplet 103. As published their key does not correctly handle *Rheosmittia* without a scutal tubercle. The key could be modified to incorporate *P. ferringtoni* by adding the following couplet between couplets 103 and 104:

Gonostylus straight, or at most weakly curved along its length .... *Krenosmittia*

- Gonostylus curved apically .... *Parakiefferiella ferringtoni* and *Rheosmittia* (in part)

Parakiefferiella ferringtoni cannot reliably be distinguished at the genus level from *Rheosmittia* species without a scutal tubercle except through details of the male genitalia. The genus *Hanocladius* also keys out in the same couplet (Wang and Sæther 2002), but can be distinguished from the *Parakiefferiella* group by the presence of scapellate acrostichals and acute anal point (see Discussion).

Natural history. Immatures of *P. ferringtoni* were collected from low-order Puget Sound urban streams, and the taxon is typically collected in cool, low-order streams often at low elevation, but it was also collected from two higher-elevation streams along the east side of the Cascade Mountains and from the Duckabush River on the Olympic Peninsula. In Montana *P. ferringtoni* has been recorded from mountain streams, including areas in the early stages of regrowth following fire. Most records of mature pupae are from late July or August, though this may be an artifact of collecting procedures for biomonitoring as those times are favored for sampling by agencies in western North America. There is at least one record from southwest Washington of mature pupae in April, suggesting a possible bivoltine phenology.

Key to Nearctic *Parakiefferiella* pupae

This key was adapted from Langton 1991, Langton and Visser 2003 and Langton 2023 with reference to Sæther 1969, Sublette 1970 and Cranston and Oliver 1988 for *Parakiefferiella subaterrima* Malloch and Makarchenko and Makarchenko

2010 for *Parakiefferiella rara*. We suggest cross referencing any specimens with Langton 2023, as that publication keys thirteen additional provisional taxa. The pupa of *Parakiefferiella finnmarkica* Tuiskunen, reported by Hebert et al. 2025 from Canada, is currently unknown.

1. Anal lobes without macrosetae, or if macrosetae present minute and less than 0.1x length of anal lobe, margins of anal lobes irregularly serrate .... *Parakiefferiella ferringtoni*

- Anal lobes with prominent macrosetae 0.2–0.35x anal lobe length. Margins of anal lobes not serrate 2

2. Anal lobe points >1.5x length anal lobe base, anal lobe tapering evenly from base to apex 3

- Anal lobe points <1.5x length anal lobe base, apical points of anal lobe distinctly constricted from base 4

3. Abdominal segments with lateral setae small and inconspicuous, <0.2x length of the abdominal segment .... *Parakiefferiella gracillima* Kieffer

- Abdominal segments with strong lateral setae, >0.2x length of the abdominal segment .... *Parakiefferiella rara* Makarchenko and Makarchenko

4. Thoracic horn absent .... *Parakiefferiella subaterrima* Malloch

- Thoracic horn present 5

5. Pedes spurii B absent .... *Parakiefferiella nigra* Brundin

- Pedes spurii B present 6

6. Thoracic horn smooth (without points/spinules), tergite VII with point patch of spinules .... *Parakiefferiella coronata* Edwards

- Thoracic horn with points/spinules, tergite VII without distinct point patch, though shagreen may be present 7

7. Anterior shagreen bands of tergites widely broken medially, width of gap subequal to median shagreen band... *Parakiefferiella smolandica* Brundin

- Anterior shagreen bands of tergites complete or with a narrow gap medially, if gap present much narrower than median shagreen band 8

8. Anterior shagreen band on tergite III with points smaller than those of median shagreen band .... *Parakiefferiella bathophila* Kieffer

- Anterior shagreen band on tergite III with points larger than those of median shagreen band .... *Parakiefferiella scandica* Brundin

Key to Nearctic *Parakiefferiella* adult males

This key was adapted from Cranston et al. 1989 with reference to Caldwell 1996.

1. Terminal segment of maxillary palpus length > 10x its width .... *Epoicocladius* Šulc & Zavrel

- Terminal segment of maxillary palpus < 10x its width 2

2. Gonostylus straight, or at most slightly curved evenly along its length 3

- Gonostylus distinctly curved apically 5

3. Costa extended beyond R_{4+5} .... *Krenosmittia* Thienemann & Kruger

- Costa not extended beyond R_{4+5} 4

4. Length of terminal maxillary palpomere < 2x its width, scutal tuft absent, virga present .... *Lapposmittia* Thienemann

- Length of terminal maxillary palpomere > 2x its width, scutal tuft present, virga absent .... *Acamptocladius* Brundin

5. Scutum without medial tubercle or tuft of setae .. .. *Parakiefferiella ferringtoni*

- Scutum with medial tubercle and/or tuft of setae 6

6. Scutum with medial tubercle bare of setae .... *Rheosmittia arcuata* Caldwell

- Scutum with medial tuft of setae, with or without tubercle .... other *Parakiefferiella* Thienemann

Discussion

Placement of Parakiefferiella ferringtoni

Parakiefferiella ferringtoni is aberrant and requires a revision of the diagnoses for the pupal and adult stage of its genus. In some ways it seems like an intermediate between *Parakiefferiella* and *Rheosmittia*, having more elongate anal lobe apices than most *Parakiefferiella* pupae (though *Parakiefferiella gracillima* Kieffer is longer), reduced or absent anal macrosetae, and the adult lacking a scutal tubercle or tuft. However, it has none of the distinctive synapomorphies that demarcate *Rheosmittia* in the larval and pupal stages (see below), and the only features that would preclude it from being placed in *Parakiefferiella* is the absence of a scutal tuft in the adult and anal macrosetae in the pupa.

As the presence of a scutal tubercle is variable between species of *Rheosmittia*, it is not unreasonable to suspect the homologous setal tuft may vary within *Parakiefferiella.* Similarly, variable number of minute anal macrosetae found in some specimens of *P. ferringtoni* suggest an autapomorphic reduction from the three well developed macrosetae found in "normal" *Parakiefferiella*. As the other features of *P. ferringtoni* fall within the variation already established in *Parakiefferiella* we decided to place it in that genus and emend the generic description.

Generic concepts in the Parakiefferiella group.

During the early parts of our study we believed *P. ferringtoni* may have merited placement in its own genus, but as we examined other members within the genus group it became clear that the delineations between some of the genera were based on plesiomorphies and autapomorphies. We decided to reexamine the limits of the *Parakiefferiella* group and the genera within by searching for synapomorphies to define each genus.

This was complicated by uncertainty about the nearest relatives of the *Parakiefferiella* group within Orthocladiinae. While there have been both molecular (Cranston et al. 2011) and morphological (such as Mendes et al. 2004a, 2004b, Mendes and Andersen 2008, Pinho et al. 2009, Andersen et al. 2024) phylogenies produced, each only contains a fraction of the genera of Orthocladiinae and there are substantial differences in relationships between the various phylogenies. The morphological phylogenies have consistently recovered *Parakiefferiella* and *Krenosmittia* as sister taxa when both have been included, but most of the other genera historically included in the *Parakiefferiella* group have never been included in computational morphological or molecular analyses. It is unclear what genus or group of genera represents the sister group of the *Parakiefferiella* group (or even what genera should be included within the group) without falling back on older intuitive assertions of relationships between genera.

Sæther (1983) provided a definition of the *Parakiefferiella* group containing *Epoicocladius* Šulc & Zavrel, *Gynnidocladius* Sublette and Wirth, *Krenosmittia* Thienemann and Krüger, *Lopescladius* Oliveira, *Parakiefferiella, Sætheriella* Halvorsen and *Stilocladius* Rossaro. The sole synapomorphy for grouping these species provided by Sæther (1983) was "Anal lobe of pupa with an apical more or less well-developed elongation." This was despite the fact that the immatures of *Gynnidocladius* and *Sætheriella* are unknown and the configuration of the anal lobes of *Lopescladius* and *Stilocladius* (cylindrical or rounded with apical macrosetae) are different than the anal lobes of other members of the group (having acutely pointed apices and subapical macrosetae). There are also other genera with extended anal lobes, including ones with pointed apices such as *Acamptocladius* Brundin and *Parachaetocladius* Wülker. While *Epoicocladius*, *Krenosmitta* and *Parakiefferiella* share several characters in the adult stage, the adults of the other species included in Sæther (1983) are quite heterogenous. Sæther and Andersen (1995) placed their new genus *Ionthosmittia* Sæther and Andersen in the *Parakiefferiella* group based on "wing features," including the evidently bare squama and extended costa (the immatures of *Ionthosmittia* are unknown). There have been other genera, such as *Hanocladius* Sæther and Wang (2002) and *Trondia* Ferrington and Sæther (2006), which have been noted to be similar to *Parakiefferiella* group taxa but were not explicitly included in the genus group.

A broad characterization of the *Parakiefferiella* group could be those taxa with the anal lobes terminating in acute points in the pupa and the adult male without a prominent subapical seta of the antenna, acrostichal setae absent (except for a posteriorly located medial setal tuft in some taxa), no setae on the squama and anal point broad and extending beyond the posterior margin of the epandrium. This characterization would include *Acamptocladius*, *Epoicocladius, Krenosmitta, Lapposmittia* Brundin, *Parakiefferiella, Rheosmittia* and probably *Lappokiefferiella* Tuiskunen and *Qiniella* Wang and Sæther (for which pupae are unknown). This excludes *Lopescladius* by the blunt apex of the anal lobe and absence of the anal point (Sæther 1983, Caldwell 1996), *Sætheriella* and *Ionthosmittia* by the presence of acrostichals (Halvorsen 1982, Sæther and Andersen 1995) and *Stilocladius* by the presence of acrostichals, rounded apex of the anal lobe and elongate, acute anal point (Sæther 1982, Coffman et al. 1986). Cranston et al. 2011 recovered *Lopescladius* as sister to *Stictocladius* and related to the *Brillia* group of genera rather than the *Parakiefferiella* group in their molecular study. *Gynnidocladius* is harder to ascertain based on the original description (Sublette and Wirth 1980), the curved apex of the gonostylus is found in some *Parakiefferiella* group taxa and it appears that the acrostichals are absent in their illustration of the thorax (though this feature is not mentioned in the text of the description). However, the anal point does not extend beyond the posterior margin of the epandrium (Sublette and Wirth 1980) which would exclude it from our concept of the group. For the purpose of this discussion we will not treat *Gynnidocladius*, though it, *Ionthosmittia* and *Sætheriella* merit reexamination when additional material becomes available – especially the immature stages.

Delimitation of genera in the Parakiefferiella group and morphological characters of phylogenetic significance

As described above, the *Parakiefferiella* group is herein broadly characterized as those taxa with the anal lobes terminating in acute points in the pupa, and the adult male without a prominent subapical seta of the antenna, few or no acrostichal setae, no setae on the squama and anal point broad and extending beyond the posterior margin of tergite IX. This characterization would include *Acamptocladius*, *Epoicocladius, Krenosmitta, Lapposmittia, Parakiefferiella, Rheosmittia* and probably *Lappokiefferiella* and *Qiniella* (for which pupae are unknown). Putative synapomorphies to support each genus follow:

Acamptocladius: Larva with dorsomentum toothed, separated medially by hyaline ventromentum. Pupa with L setae on posterior segments branched apically (also found in *Parametriocnemus* Goetghebuer). Adult with virga absent (shared with numerous other genera outside the *Parakiefferiella* group).

Epoicocladius: Larva with long dark body setae, large procerci, mentum with 4-8 median teeth. Pupa with dense fringe of long lateral setae on abdomen. Adult with long terminal maxillary palpomere (>10x width).

Krenosmittia: Larva with elongate maxillary palp, at least one anal seta longer than ¼ body length (shared with *Parachaetocladius* and *Pseudorthocladius*). Pupa with prominent rows of spines on posterior margins of abdominal tergites and sternites (shared with numerous other genera outside the *Parakiefferiella* group). No adult synapomorphies.

Lappokiefferiella: Larva and pupa unknown. No adult synapomorphies.

Lapposmittia: Larva and pupa without unambiguous synapomorphies. Adult with terminal maxillary palpomere length >2x width (also found in some species of *Ionthosmittia*, Sasa and Okazawa 1994, Yamamoto et al. 2015).

Parakiefferiella: Larva with six antennal segments (shared with other genera, ambiguous depending on interpretation of *Rheosmittia* antenna).

Qiniella: Larva and pupa unknown. Adult with trifid gonostylus.

Rheosmittia: Larva with elongate antenna with partially desclerotized break in second article, premandible with numerous comb-like teeth, hyaline mentum, and flattened, toothed hypopharyngeal scales. Pupa with flattened D5 setae on abdominal tergites. No adult synapomorphies.

Our review thus found six of the genera had at least one putative synapomorphy, but *Parakiefferiella* appears to be defined by symplesiomorphies shared with some of the other genera. *Lappokiefferiella* is dubiously distinct, defined by a lack of features (lack of extended costa and presence of a virga) that would allow placement in one of the established genera as the immature stages are unknown. Understanding the placement of *P. ferringtoni* within the genus and placement of *Parakiefferiella* within *Parakiefferiella* group requires systematic revision of the group, ideally using integrative taxonomic methods. Establishing reliable relationships within the *Parakiefferiella* group will require more comprehensive genus sampling than is available in previous morphological and molecular phylogenies of the subfamily. Such a project is outside the scope of the current study, but in our investigation we found many morphological characters representing synapomorphies to define genera or of potential utility in resolving relationships both within and between genera. Without an unambiguous sister taxon to *Parakiefferiella* it is impossible to establish polarity for many of these morphological characters, but we include discussion of these characters even if their relevance to the phylogeny remains unclear.

Larvae

Larval antenna with terminal flagellomere minute and hair-like. *Parakiefferiella* and *Rheosmittia* have a hair-like terminal flagellomere (Andersen et al. 2013), the 6th antennal article in *Parakiefferiella* and the fifth in *Rheosmittia*, suggesting the close relationship of these taxa. There are more distantly related orthoclad genera (*Parametriocnemus*, *Oropuella* and *Stilocladius* among others) that also have hair-like terminal flagellomeres (Andersen et al. 2013, Fasbender 2020).

Number of larval antennal flagellomeres. Larvae of the *Parakiefferiella* group have from four to six flagellomeres, the number of which seem to be consistent within genera. *Epoicocladius* and *Krenosmittia* have four flagellomeres, *Acamptocladius, Lapposmittia* and *Rheosmittia* five, and *Parakiefferiella* six (Andersen et al. 2013). Having six flagellomeres is the only putative synapomorphy we could find for *Parakiefferiella*, though the unusual structure of *Rheosmittia*'s second flagellomere (elongate, Lauterborn organs absent; Cranston and Sæther 1986, Caldwell 1996) may represent a fusion of flagellomeres 2 and 3. If so, the *Rheosmittia* antenna form could derived from the *Parakiefferiella* type.

Antennal length <25% head capsule length; Antennal length >25% head capsule length. The elongate antenna of *Rheosmittia* (Andersen et al. 2013), along with the unusual structure of the second article as described above, are synapomorphies defining that genus.

Premandible with 1–2 apical teeth; with 3–4 apical teeth; with numerous comb-like teeth. Epoicocladius, Krenosmittia and *Parakiefferiella* have 1–2 apical teeth on the premandible (Andersen et al. 2013), which is probably the ancestral condition of the *Parakiefferiella* group. *Acamptocladius* and *Lapposmittia* have 3–4 apical teeth (Andersen et al. 2013), a potential synapomorphy uniting those genera. *Rheosmittia* has numerous fine teeth on the premandible (Andersen et al. 2013), which could potentially indicate a relationship with *Acamptocladius* + *Lapposmittia*, but also could be an independently derived condition related to its psammophilic habits.

Larval maxillary palp length < 2.5x width; > 2.5x width. The sole unambiguous synapomorphy we could find for *Krenosmittia* is the elongate maxillary palp of the larva (Sæther 1983), at least 2.5x longer than wide. The maxillary palp is as long or longer than the length from the mola of the mandible to the tip of its apical tooth. In all other genera within the *Parakiefferiella* group the length of the larval maxillary palp is less than 2.5x its basal width.

Hypopharynx without flattened scales; hypopharynx with pair of flattened, toothed scales. The development of a pair of large hypopharyngeal scales (Andersen et al. 2013) is an autapomorphy unique to *Rheosmittia* probably related to its psammophilic lifestyle.

Larvae with median and lateral portions of mentum contiguous; toothed lateral portions of dorsomentum distinctly separated by hyaline ventromentum medially; mentum completely hyaline. The genus *Acamptocladius* is unique among the *Parakiefferiella* group in having the dorsomentum divided, divided by a hyaline area of ventromentum (Andersen et al. 2013). In Orthocladiinae this is also found in *Trichochilus* (Andersen et al. 2013), which does not appear to be closely related, and Orthocladiinae sp. C Sæther (1982). The undescribed pupa of Orthocladiinae sp. C is very similar to *Acamptocladius* and *Parakiefferiella* (Epler 2001), suggesting it is a member of the *Parakiefferiella* group – possibly an undescribed species of *Acamptocladius.*

Only *Rheosmittia* has a completely hyaline mentum, but its structure (dorso- and ventromentum not separate, at most fifteen teeth, no untoothed gap medially (Andersen et al. 2013) suggest it was derived independently of the condition found in *Acamptocladius*.

Larvae with 15 or fewer teeth on the mentum; more than 15 teeth on the mentum. Most taxa in the *Parakiefferiella* group have fifteen or fewer teeth on the mentum, while *Acamptocladius, Epoicocladius* and *Lapposmittia* have sixteen or more (Andersen et al. 2013), a potential synapomorphy linking those taxa. Additionally, *Epoicocladius* has 4–6 median teeth of the mentum set in a linear row, which is a clear synapomorphy defining that genus.

Larvae without strong setae on abdomen; with strong setae on abdomen. Epoicocladius is the only member of the *Parakiefferiella* group with strong body setae as larvae (Andersen et al. 2013), another synapomorphy supporting its distinctness.

Procerci cylindrical, <25% the length of the anal tubules and not heavily sclerotized; procerci conical, >50% the length of the anal tubules and heavily sclerotized. The large, conical and heavily sclerotized procerci are a synapomorphy defining *Epoicocladius*.

At least one anal seta 25% of larval body length. Only *Krenosmittia* larvae have elongate anal setae within the *Parakiefferiella* group (Andersen et al. 2013). Mendes and Andersen 2008 recovered the *Parakiefferiella* group as sister to the *Pseudorthocladius* group (*Doithrix, Georthocladius, Parachaetocladius* and *Pseudorthocladius*; Sæther and Sublette 1983) in a reweighted parsimony analysis of their morphological dataset – though this relationship was not found in the original unweighted analysis. *Parachaetocladius* and *Pseudorthocladius* are the other two genera with elongate anal setae as larvae, and if the *Parakiefferiella* and *Pseudorthocladius* groups are sister taxa the presence of elongate anal setae could be a symplesiomorphy and provide support to *Krenosmittia* being sister to the remainder of the *Parakiefferiella* group.

Pupae

Thoracic horn absent; elongate; ovoid. The presence/absence of thoracic horns is highly variable between and within genera of Orthocladiinae, and as such is a poor indicator of relationships. When present, the thoracic horn of most orthoclads is distinctly elongate, rather than ovoid as found in *Epoicocladius*, most *Parakiefferiella* and some *Acamptocladius*. However, ovoid thoracic horns are also found in *Parorthocladius* and some *Euki-*

efferiella (Coffman et al. 1986) – suggesting this character is potentially susceptible to homoplasy.

Thoracic horn with scale-like texture. Many Orthocladiinae have pointed spicules covering at least part of their thoracic horn including most of the *Parakiefferiella* group (Sæther 1983). In many species of *Parakiefferiella* this texture has become distinctly rounded, as can be found in *P. ferringtoni,* which may indicate relationships within *Parakiefferiella*.

Posterior margins of abdominal tergites and sternites with spines or strong spinules. Krenosmittia is the only member of the *Parakiefferiella* group with rows of erect triangular spines on the posterior margins of its abdominal tergites and sternites, though this character is found in several other genera (Coffman et al. 1986). Most notable is the *Pseudorthocladius* group, recovered as sister to the *Parakiefferiella* group by Mendes and Andersen (2008).

Some species of *Parakiefferiella*, including *P. ferringtoni*, have darkened subacute spinules along the posterior margins of the abdominal tergites, which may indicate relationships between them.

Posterior margin of Tergite II with medial spine patch. Hooklets on the posterior margin of Tergite II are found in the pupae of Chironominae, suggesting that the presence of hooks or spines in the same area is plesiomorphic for Orthocladiinae – though the presence and type of hooks/spines are quite variable throughout the subfamily (Coffman et al. 1986). *Lapposmittia, Rheosmittia* and some *Parakiefferiella* (including *P. ferringtoni*) lack spines at the posterior margin of Tergite II. The polarity of this character is unclear.

Abdominal segments with three or fewer strong L *setae; with four or more strong* L *setae; with complete setal fringe. Acamptocladius* and *Lapposmittia* have four strong L setae on their posterior abdominal segments (Coffman et al. 1986), a potential synapomorphy uniting the two taxa. The L setae on segment VIII of *Acamptocladius* are additionally bifid (Coffman et al. 1986), a synapomorphy defining that genus. *Epoicocladius* has a uniform setal fringe on the lateral margins of its abdominal segments (Coffman et al. 1986), again serving as a diagnostic synapomorphy. The development of more extensive chaetotaxy on the abdomen could be a synapomorphy grouping these three taxa.

D_5 *seta trichoid;* D_5 *seta flattened and leaflike. Rheosmittia* is the only orthoclad with flattened, leaflike dorsal setae on the abdominal tergites (Coffman et al. 1986), a synapomorphy of the genus.

Anal lobes with serrations or spinules apically. Rheosmittia and some species of *Parakiefferiella* (including *P. ferringtoni*) have serrations/spines on the apical portion of the anal lobe (Langton 2023). This could be an indication of the close relationship between these taxa.

Margins of anal lobe straight; rounded basally. Krenosmittia, Rheosmittia and some species of *Parakiefferiella* such as *P. ferringtoni* and *P. gracillima* have the lateral margin of the anal lobe largely straight or evenly tapering to the apex (Coffman et al. 1986). The other taxa of the *Parakiefferiella* group have the lateral margin at the base of the anal lobe rounded, swelling somewhat laterally (Coffman et al. 1986). Based on the distribution of other characters within the *Parakiefferiella* group, the straight lateral margin was probably not homologous between *Krenosmittia* and the other taxa with that character state, though it may be a synapomorphy between *Rheosmittia* and those aberrant *Parakiefferiella.*

Anal lobe macrosetae present; reduced or absent. All members of the *Parakiefferiella* group have three macrosetae except for *Rheosmittia* (Coffman et al. 1986). There other informal taxa keyed by Langton (2023), either unplaced to genus (Orthocladiinae gen? sp? NA7 and NA8) or placed as *Parakiefferiella* (*P.* NA2 and NA3) that have a reduced number of anal setae or lack them entirely. *Parakiefferiella ferringtoni* has a variable number of reduced anal setae, suggesting there may be an evolutionary series leading to the reduction and finally absence of macrosetae.

Adults

Eye without ommatrichia; eye with ommatrichia. Rheosmittia is the only genus of the *Parakiefferiella* group with ommatrichia, though *Parakiefferiella scandica* Brundin also has them (Cranston and Sæther 1986), another instance of the blurred delineation between *Parakiefferiella* and *Rheosmittia*.

Adult male terminal maxillary palpomere length 2-10x width;<2x width; >10x width. Most taxa within the *Parakiefferiella* group have a "normal" terminal article of the maxillary palp 3–6x longer than wide (Cranston et al. 1989). *Lapposmittia* has a shortened apical palpomere <2x length/width (Cranston et al. 1989), which is probably an adaptation to its Arctic habitat, much as the male antenna has a reduced number of flagellomeres and lacks a plume. The elongate maxillary terminal palpomere of *Epoicocladius* (>10x length/width, Cranston et al. 1989) is clearly synapomorphic for that genus.

Scutum with tubercle or tuft. Acamptocladius, Epoicocladius, Lappokiefferiella and most *Parakiefferiella* have a tuft of setae located medially on the scutum (Cranston et al. 1989, Tuiskunen 1986), while some species of *Rheosmittia* have a tubercle in the same location (Caldwell 1996, Cranston and Sæther 1986, Cranston et al. 1989). This character is probably a synapomorphy for these genera, and its absence in *P. ferringtoni* and some *Rheosmittia* are probably reversals – suggesting that its absence in *Lapposmittia* may not be an indicator to exclude that genus from close relationship with *Acamptocladius*. Whether the structure presents as a tuft or tubercle may have some phylogenetic utility, as most of these groups have a setal tuft while *Rheosmittia* has a tubercle with no tuft. Interestingly, *Parakiefferiella coronata* Edwards has a combined tubercle and tuft, suggesting that the structure may have started as a setal tuft and then transitioned into a tubercle within *Parakiefferiella*.

Costa extending beyond $R_{4+5.}$ *Acamptocladius, Lappokiefferiella* and *Lapposmittia* have the costa ending at R_{4+5}, while *Epoicocladius, Krenosmittia, Parakiefferiella, Qiniella* and *Rheosmittia* have C extending beyond R_{4+5} (Cranston et al. 1989). It is unclear which state represents the plesiomorphic condition within the group, and this character is variable between species in many genera outside the *Parakiefferiella* group (Cranston et al. 1989). The state of this character is unknown for *P. ferringtoni*, as we only had pharate specimens for examination.

Gonostylus curved apically. Having the apex of the gonostylus curved apically is a putative synapomorphy of *Parakiefferiella* + *Rheosmittia*. However, this character is found in unrelated orthoclads (ex. *Heleniella curtistyla* Sæther) and is subject to interpretation, as the apparent degree of curvature of the gonostylus can differ between specimens of the same species.

Gonostylus undivided; Gonostylus trifid. Qiniella is known solely from adults, defined by the male having a trifid gonostylus. Wang and Sæther (1998) noted in the initial description of the genus that they resembled *Krenosmittia* except for said distinctive gonostylus. As *Krenosmittia* adults are diagnosed within the *Parakiefferiella* group solely by plesiomorphies, this suggests *Qiniella* is outside the *Acamptocladius, Epoicocladius, Lappokiefferiella, Parakiefferiella, Rheosmittia* lineage. As the genus is based only on a single adult autapomorphy and the immatures are unknown *Qiniella* deserves further investigation as to whether it truly represents a distinct genus or just an unusual species group within one of the other genera.

Virga present; absent. All taxa within the *Parakiefferiella* group have a virga except *Acamptocladius* (Cranston et al. 1989), its absence is thus a synapomorphy of that genus.

The monophyly of Parakiefferiella and status of Lappokiefferiella and Rheosmittia.

Parakiefferiella been noted as in need of revision in North America (Epler 2001, Namayandeh pers. comm.) with many undescribed species and possible conspecificity of European names with Nearctic taxa (Epler 2001). Epler keyed seven larval taxa from the southeast United States, while Langton (2023) keyed seventeen pupal taxa, thirteen unnamed. With the description of *P. ferringtoni* there are only six named species of *Parakiefferiella* recorded from North America.

Understanding the diversity of *Parakiefferiella* is complicated by the ambiguous characters used to diagnose the genus. During our study we were able to find only one potential unambiguous synapomorphy for the genus, the presence of six larval flagellomeres. This is a very weak character, especially as the structure of *Rheosmittia*'s antenna could be derived from the *Parakiefferiella* configuration by the fusion of flagellomeres 2 and 3 as described above. The other characters used to diagnose *Parakiefferiella* within the genus group are: scutal tuft present, costa extended beyond R_{4+5}, and the gonostylus curved apically. The scutal tuft is shared with several other genera, and the evidently homologous tubercle seen in *Rheosmittia* can also be found in *P. coronata*. The extended costa is shared with *Epoicocladius, Krenosmittia* and *Rheosmittia*; if *Krenosmittia* is sister the remainder of the *Parakiefferiella* group this may represent a plesiomorphy. The curved gonostylus appears to be a synapomorphy within the *Parakiefferiella* group, but is shared with *Lappokiefferiella* and *Rheosmittia*. We are thus led to ask, is the current concept of *Parakiefferiella* paraphyletic if *Rheosmittia* and possibly *Lappokiefferiella* are treated as separate genera?

Rheosmittia is clearly a monophyletic group, with several synapomorphies related to its specialization in sand substrates during the immature stages as noted above. The curved gonostylus has been used to suggest a close relationship between *Rheosmittia* and *Parakiefferiella*, but as noted above the characters that separate *Parakiefferiella* are symplesiomorphies. There is one character of the larval mouthparts that could suggest a relationship between *Rheosmittia* and *Acamptocladius* + *Lappokiefferiella* (more than two apical teeth on the premandible), but this evidence seems weak since *Rheosmittia* has far more teeth in a comb-like arrangement that could have been independently derived from its psammophilic lifestyle. In our opinion the thread like terminal antennal flagellomere in the larva, curved gonostylus, and the reduction or absence of anal lobe macrosetae in the pupae of some *Parakiefferiella* indicate a closer relationship between that taxon and *Rheosmittia.* The reduction of anal lobe macrosetae, narrowing of the basal part of the anal lobe and serrations on the apical part of the anal lobe as found in *P. ferringtoni, P. gracillima* and some undescribed *Parakiefferiella* suggest an evolutionary series leading to *Rheosmittia*. Thus, we present the hypothesis that *Rheosmittia* is probably a morphologically divergent specialist lineage within *Parakiefferiella* as the latter is currently defined.

Lappokiefferiella is another enigmatic lineage which confounds our understanding of *Parakiefferiella*. Being known solely in the adult stage has hindered placement of *Lappokiefferiella platytarsus,* described in a monotypic genus because the species could not be conclusively placed between *Acamptocladius, Lapposmittia* or *Parakiefferiella* (Tuiskunen and Lindeberg, 1986). The species was excluded from *Acamptocladius* by the presence of a virga, and *Parakiefferiella* by the absence of a costal extension. Both characters have been found to be variable within genera outside the *Parakiefferiella* group (Sæther and Wang 1995, Cranston et al. 1989). It lacks the reduced antennal plume and small terminal segment of the maxillary palp found in *Lapposmittia*, though those are autapomorphies probably related to adaptations to the arctic environment as seen in numerous other groups. The gonostylus appears somewhat curved apically, which could indicate this species is just another aberrant *Parakiefferiella*, as the extent of costal extension is variable in genera outside the *Parakiefferiella* group. Being defined solely by a lack synapomorphies and lacking autapomorphies of its own, *L. platytarsus* is possibly an aberrant species of one of the three aforementioned genera. Finding the immature stages should settle the placement of this species.

The current generic classification of Orthocladiinae needs substantial revision, as many genera are based on non-cladistic morphological character formulae instead of synapomorphies. This limits the utility of genera, since many are artificial and potentially unstable assemblages of species. Numerous genera have been described based on autapomorphic characters without consideration of whether they may represent a derived group within another genus, while others have been established for species that do not fit an existing generic diagnosis or “don’t key out properly.”

While we encountered non-cladistic genera in the *Parakiefferiella* group, the problem is by no means limited to this group. Most groupings of orthoclad genera the first author examined in detail contain probable paraphyletic taxa and genera defined by non-synapomorphies to more or less of an extent. Resolving these issues is complicated by the fact that there has yet to be a definitive phylogeny covering the majority of genera in the subfamily, which is needed to provide a backbone to understand character polarity and discover proper synapomorphies. This has created something of a “chicken and egg” conundrum: to create an accurate phylogeny to understand generic synapomorphies requires revision at the species level, yet to properly place species in genera requires a cladistic framework.

Conclusion

Parakiefferiella ferringtoni is an unusual species of *Parakiefferiella* found in the Western U.S. Amended keys for all three life stages of Nearctic *Parakiefferiella* including *P. ferringtoni* should aid in taxonomic and ecological research. Documenting and describing this species uncovered problems with how genera are delineated in the *Parakiefferiella* group. While six of the eight genera we included within the group appear monophyletic, *Parakiefferiella* is probably paraphyletic with *Rheosmittia* as a specialized psammophilic lineage arising within it. *Lappokiefferiella* is dubiously distinct, and discovery of the immature stages should help solidify the placement of that monotypic genus.

Acknowledgements

We thank Hongqu Tang for sharing his observations on phylogeny of the *Parakiefferiella* group, along with Armin Namayandeh for discussion of the Nearctic *Parakiefferiella*. Will Bouchard, Hongqu Tang and an anonymous reviewer provided feedback that improved this manuscript. Chad Larson (Washington Department of Ecology) and Kate Macneale (King County Department of Natural Resources) and the Montana Department of Environmental Quality provided access to material for this study.

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Article submitted 30. January 2025, accepted by Corrie Nyquist 11. July 2025, published 15. November 2025.