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CHIRONOMIDAE (DIPTERA) OF THE COLORADO RIVER, GRAND CANYON, ARIZONA, USA,

I: SYSTEMATICS AND ECOLOGY

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ABSTRACT.—We describe the chironomid midge fauna of the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. This depauperate fauna, consisting of 38 species, is dominated by euryecious Nearctic or Holarctic orthocladine taxa. In addition, a small Neotropical faunal component is represented by *Polypedilum obelos* Sublette & Sasa and *Rheotanytarsus hamatus* Sublette & Sasa.

The following new synonyms are given: *Protenthes riparius* Malloch 1915 with *Tanypus bellus* Loew 1866 [=*Procladius (Psilotanypus) bellus* (Loew)]; *Cricotopus olivetus* Boesel 1983 with *Cricotopus (Cricotopus) annulator* (Goetghebuer) 1927; *Cricotopus edurus* Sublette & Sublette 1971 with *Orthocladius infuscatus* Malloch 1915 [=*Cricotopus (Cricotopus) infuscatus* (Malloch)]; *Cricotopus subfuscus* Sublette & Sublette 1971 with *Orthocladius infuscatus* Malloch 1915 [= *Cricotopus (Cricotopus) infuscatus* (Malloch)]. The following new species are described: *Cricotopus (Cricotopus) blinni* Sublette, *Cricotopus (Cricotopus) herrmanni* Sublette, *Metriocnemus stevensi* Sublette, and *Cladotanytarsus marki* Sublette. We discuss the distribution and ecology of each chironomid species collected in this large, regulated, aridlands river.

Key words: Chironomidae, Colorado River, distribution, euryecious species, Glen Canyon Dam, Grand Canyon, midges, new species, synonymies.

Although chironomid midges are often numerically dominant aquatic macroinvertebrates in large river ecosystems, relatively few taxonomic studies have been conducted in the American West. The known distributions of chironomids in western North America are principally based on individual species records in various works and on comprehensive studies by Sublette (1960, 1964) and Sublette and Sublette (1979). Sublette and Sublette (1979) report on material from headwater reaches of the Colorado River in the upper San Juan and Gila drainages of New Mexico. Cowley (1995) examines the chironomid fauna of the upper Rio Grande, and Ruse et al. (unpublished data) identify several chironomid species in the headwaters of the Arkansas River in Colorado; both studies report species that also occur in the Colorado River. Wolz and Shiozawa (1995) identify chironomid genera of the upper Green River in low-velocity habitats at the Ouray National Wildlife Refuge, Utah, and relate flow

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velocity to assemblage structure. Spindler (1996) reports on chironomid distribution in 10 tributaries in Grand Canyon. Also, Pearson (1967) and Rader and Ward (1988) describe the invertebrate fauna of the Green River near Flaming Gorge Dam and in the upper Colorado River, respectively.

Chironomid midges are abundant in the Colorado River in Grand Canyon (Leibfried and Blinn 1986, Blinn et al. 1992, Stevens et al. 1997). This is the largest river in the American Southwest, flowing 2250 km from the Rocky Mountains to the Sea of Cortez, and it is heavily regulated by numerous diversions and impoundments (Hirsch et al. 1990). However, no study of chironomid taxonomy has been conducted in Grand Canyon.

In this paper we describe and review the taxonomy and ecology of chironomid species in the Colorado River between Glen Canyon Dam and Lake Mead, including the entire Grand Canyon section of the river. Because our collections are primarily from the mainstream corridor, additional collecting in tributary streams, springs, and seeps will greatly increase the number of species recognized in Grand Canyon (cf. Spindler 1996).

METHODS AND MATERIALS

Study Area

The Colorado River flows 475 km from the base of Glen Canyon Dam (975 m elevation) to Lake Mead (350 m elevation) through Sonoran and Mojave Desert terrain, through lower Glen Canyon and all of Grand Canyon (Turner and Karpiscak 1980; Fig. 1). By convention, locations along the Colorado River are designated in river miles from Lees Ferry. The river passes through 13 bedrock-defined geomorphic reaches, and the Paria (km 1) and Little Colorado (km 98) rivers create 3 turbidity segments (Schmidt and Graf 1990, Stevens et al. 1997).

Field Methods

Adult and pharate aquatic Chironomidae were collected throughout the year in 1976–77 and 1990–91 by sweep-netting riparian vegetation (mostly *Salix exigua* Nutt., *Tamarix ramosissima* Loureiro, and *Baccharis* spp.), white and UV light-trapping, dip-netting, and larval rearing from benthic spot and quantitative samples (Stevens et al. 1997).

Taxonomy

Taxonomic determinations and descriptions were made by J.E. Sublette. Specimens from Grand Canyon which are new to science, and which also occur in other river systems, have been included in the type series of the new species described here. Some adult specimens that had been collected by sweep-netting may be associated with tributaries or springs; however, many individual larvae collected from the river were reared to emergence for identification.

Most of the morphological terminology used here follows Sæther (1980); however, in the Orthocladiinae the genitalia appendages were named by position rather than homology inferred by Sæther (1980). We term the superior volsella the basimedian gonocoxite lobe, and the inferior volsella is here referred to as the basidorsal and basiventral gonocoxite lobes. We followed Sæther's terminology for Chironominae genitalia. The terms *bacatiform papillae* and *nasiform tubercles* for structures on the pupal wing sheath are employed for *perlen* and *nasen*, respectively (Sublette and Sasa 1994). The basal palpomere of adult chironomids is weakly chitinized and frequently partially collapsed; consequently, only measurements for the apical 4 palpomeres are given. The term *temporal setae* here includes both the postorbital and outer vertical setae. If the frontal setae are continuous with temporals, they are also included. The length ratio of the gonocoxite to the gonostylus is given as Gc/Gs; gonocoxite length is measured along the ventral midline of the gonocoxite. In the pupa the anal lobe ratio (ALR; Soponis 1977) is the length of the longest anal macroseta divided by the anal lobe length. Ventral head length of the larva is measured from the medial apex of the mentum to the outer edge of the occipital ring.

In descriptions of new species, morphometric and meristic features of the holotype male are listed first, with the range of variation for paratypes and the number upon which the statistic is based provided parenthetically unless the holotype was unique. In other species descriptions the range is given with the number of specimens upon which the statistic is based, listed in parentheses immediately following.

The original citation is given in each species description, along with references to subsequent studies of that species. If a species has

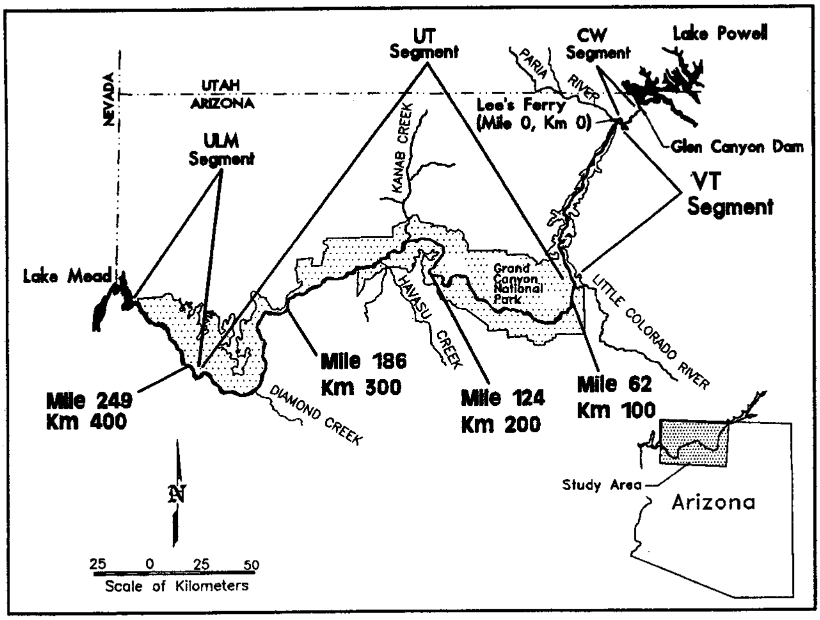


Fig. 1. Map of the study area between Lake Powell and Lake Mead, Arizona, showing 13 geomorphic reaches (Schmidt and Graf 1990) and 3 turbidity segments (Stevens et al. 1997): CW = clearwater segment, VT = variably turbid segment, and UT = usually turbid segment. Also shown is upper Lake Mead (ULM), a usually turbid, lacustrine segment.

been reviewed or revised, literature listed in that study is not included.

Deposition of type material is indicated by the following abbreviations: California Academy of Science, CAS; United States National Museum of Natural History, USNM; Academy of Natural Sciences of Philadelphia, ANSP; Illinois Natural History Survey, INHS; American Entomological Institute, AEI; University of California–Riverside, UCR; University of Colorado, U of C; University of Minnesota, UMN; Brigham Young University, BYU; James E. Sublette collection, JES; Scott J. Herrmann collection, SJH. Non-type material collected in Grand Canyon, unless otherwise indicated, is retained at Northern Arizona University.

Ecology

We review existing information on the ecology of North American Chironomidae and provide some additional data from our collections. In those cases where a species has a Holarctic distribution, selected reference to the European literature is made. Two regional biotic indices have been developed in North America, based on water quality and chironomid distribution. The North Carolina biotic index (NCBI; Lenat 1993) references Hilsenhoff's Wisconsin biotic index (Hilsenhoff 1977, 1982, 1987, 1988); therefore, only the NCBI is cited here. The NCBI, based on larvae from macrobenthic samples, lists only species groups because the taxonomy of non-adult chironomids is less definitive. The NCBI is based on a range of 0–10, with 0 being the most intolerant to pollution and 10 the most tolerant. As Lenat (1993) indicates, comparisons between different geographic regions may be uncertain; nevertheless, because citation of ecological tolerances from other regions may have value for broad-ranging species, it is provided here.

TAXONOMIC DESCRIPTIONS

Subfamily Tanypodinae

Procladius (Psilotanypus) bellus (Loew)

Tanypus bellus Loew 1866:4; type locality, D.C.

Protenthes riparius Malloch 1915:389; type locality, Thompson's Lake, Havana, IL. *New synonym.*

Procladius riparius (Malloch); Roback 1971:167, holotype male.

Procladius bellus (Loew); Kowalyk 1985:88, larval morphology.

Procladius (Psilotanypus) bellus (Loew); Roback 1971: 162, revision, synonymy, adults; 1980:31, larva and pupa; Sublette and Sublette 1979:61, in list; Parkin and Stahl 1981:122 and Stahl 1986:70, ecology; Hudson et al. 1990:5, in list; Oliver et al. 1990:15, in catalog; Epler 1995:3.54, larva.

DIAGNOSIS.—Adults: Keyed from other members of the Nearctic fauna by Roback (1971); larva and pupa keyed by Roback (1980). Adults range from almost black (early season collections or at higher elevations or latitudes) to pale yellow with pale orange-brown vittae.

DISCUSSION.—*Procladius riparius*, here synonymized with *P. bellus*, is a typical dark form except for genitalia (Roback 1971). Examination of specimens from within the range of Malloch's original material suggests that pinned specimens and genitalia mounts were mixed, with the genitalia nominally associated with the pinned holotype of *P. riparius* actually being that of *Coelotanypus concinnus* (Coquillett). Both species occur in central U.S. and, presumably, the specimens were inadvertently switched when slides from the collection were mounted. Malloch's presumptive holotype *P. riparius* genitalia were illustrated by Roback (1971: Figs. 254, 255) with a double megaseta, a condition that has been observed frequently in *C. concinnus* but not in species of *Procladius (Psilotanypus)*. Roback (1971) synonymized the paratypes of *P. riparius* but not the holotype, because of the peculiar genitalia.

ECOLOGY.—Typically, *P. bellus* occurs in the littoral zone of lakes and reservoirs (Sublette 1957, Rosenberg et al. 1984) or other shallow lentic water (Wrubleski 1987, Wrubleski and Rosenberg 1990), in slow-moving streams, and along backwater areas of faster moving streams. It was uncommon in a Laurentian stream system, occurring in quiet water on finer sediments with vegetation (Cloutier and Harper 1978), and rare, comprising only 0.4% of Tanypodinae males/m^2/yr, in a brown-water stream in Alberta (Boerger 1981). Ferrington and Crisp (1989) reported that this species is characteristic of the recovery region below enrichment zones produced by wastewater treatment plant effluents in 2 small streams in Kansas. In the upper Arkansas River, Colorado, adults were taken at 1444–1618 m elevation (Ruse et al. unpublished data). The single Grand Canyon specimen was collected near the inflow into Lake Mead during high lake level.

DISTRIBUTION.—Widely distributed in North America.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 269.5, 365 m elev.

SUBFAMILY DIAMESINAE

Diamesa heteropus (Coquillett)

(Figs. 2–5)

Tanypus heteropus Coquillett 1905:66; type localities, Washington, New Mexico, and New Hampshire (Hansen and Cook [1976] suggest the type series was mixed).

Diamesa heteropus (Coquillett); Hansen and Cook 1976:95, revision, synonymy, distribution; Sublette and Sublette 1979:64, in list; Ferrington 1983:106, distribution; Herrmann et al. 1987:321, distribution; Oliver et al. 1990:17, in catalog.

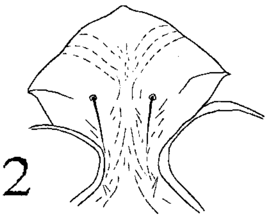
PUPA.—The pupa has been known previously (Hansen and Cook 1976) but not described. Exuviae entirely pale brown to dark brown. Abdomen length 3.32–6.11 mm.

Cephalothorax: Large frontal setae present on the frontal apotome (Fig. 2); length 139–281 µm. Thoracic horn (Fig. 3), length 359–515 µm. Median suture with moderate tubercles on either side. Precorneal setae 2, of unequal length, with the longer being 139–281 µm. Dorsocentrals 3, small, almost in a line, with the anterior seta being largest. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Spine pattern (Fig. 4). Anal lobe (Fig. 5); anal macrosetae length 289–372 µm; ALR 0.79–0.84.

DIAGNOSIS AND DISCUSSION.—The combination of hairy eyes, plumose antenna, and distinctive genitalia (Hansen and Cook 1976: Fig. 113) serves to differentiate the male. The pupal armature (Fig. 4) appears distinctive among western *Diamesa*. Tergal and sternal spines are similar to those of *Diamesa incallida* (Walker) (cf. Sæther 1969: Fig. 13, as *Diamesa fonticola* Sæther), but that species lacks the well-developed spines on tergum II of *D. heteropus*. The *Diamesa haydaki* Hansen pupa (previously undescribed) has a similar armature, but the sternal spines are more slender and are dark to the base (best observed on T V–VII).

ECOLOGY.—*Diamesa heteropus*, the most common species of *Diamesa* in western North America, inhabits cool to cold streams, including spring runs, on cobble-gravel-sand bottoms. In the upper Arkansas River of Colorado it has been taken from near the headwaters to Pueblo Reservoir at elevations of 1431–2905 m (Ruse et al. unpublished data). In New Mexico it is widely distributed below elevations of 2000 m, usually emerging from September through March (Sublette and Sublette 1979).



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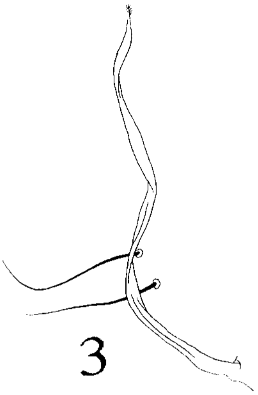

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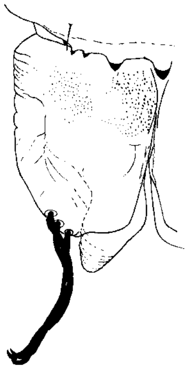

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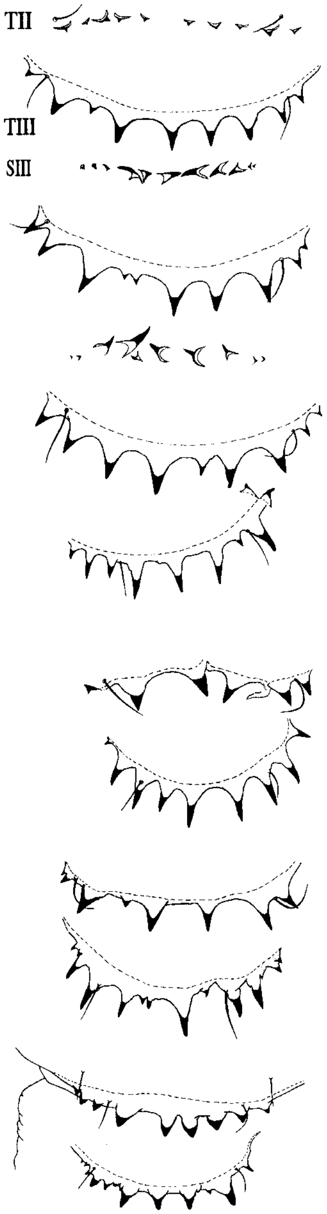

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Figs. 2–5. *Diamesa heteropus.* Pupa: 2, frontal apotome; 3, respiratory horn; 4, abdominal spine pattern (the T IV/S IV–T VIII/S VIII spine sets are shown sequentially); 5, anal lobe.

The species is rare in Grand Canyon, probably due to the lack of suitable substrata throughout much of the canyon.

DISTRIBUTION.—Alaska to Minnesota, south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 specimen from river mi 61.0, 840 m elev. Reared material from New Mexico and Colorado was also examined.

SUBFAMILY ORTHOCLADIINAE

Cardiocladius platypus (Coquillett)

(Figs. 6–9)

Orthocladius platypus Coquillett 1902:93; type locality, Flagstaff, AZ.

Cardiocladius platypus (Coquillett); Sublette 1966:587, review; Oliver et al. 1990:21, catalog.

Because the original description by Coquillett (1902) and redescription by Sublette (1966) were based on an imperfect pinned holotype, the following data are provided to augment these descriptions.

MALE.—*Coloration*: Almost entirely blackish brown; humeral and pleural areas very slightly paler.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.51–1.63 (3). Palpal proportions 86: 156:187:250 (1) μm. Eyes reniform, with a slightly angular medial margin. Ocular ratio 0.56–0.60 (4). Clypeus rectangular, distinctly wider than high, about as wide as the antennal pedicel; clyp/ped ratio 0.96–1.20 (4); with 26–28 (4) setae. Temporal setae 8–12 (4), in a slightly staggered single row, reaching to 0.68 of the distance from the eye to midline of the head.

Thorax: Antepronotum almost parallel-sided, not produced at the dorsal apex (Fig. 6). Thoracic chaetotaxy: lateral antepronotals 7–10 (4); dorsocentrals 14–23 (5), anteriorly in a partial double row; acrostichials 13–21 (4); prealars 5–7 (5); supra-alars lacking; scutellars 30–32 (5), in a strewn pattern.

Wing: Membrane with microtrichia visible at 125X. Costa not produced beyond R_{4+5}, which ends distal to M_{3+4} at 0.22 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} evanescent at apex. Venarum ratio 1.02–1.09 (3). Wing length 1.90–2.58 (3) mm. Squama with 31–52 (4) marginal setae, which are 3–4X at base, becoming 2X, then 1X near the alula. Wing vein setae: R 9–14 (4), R_1 1–4 (4), other veins without setae.

Legs: Foretibial spur length 62–74 μm (3); middle tibial spur lengths 52–68/24–40 μm (4); hind tibial spur lengths 80–102/26–40 μm (4). Pulvilli absent. Leg ratios: P I 0.68–0.69 (3); P II 0.43–0.49 (4); P III 0.52–0.55 (3). P III comb setae 9–14 (4). P III sensilla chaetica 3–6 (2).

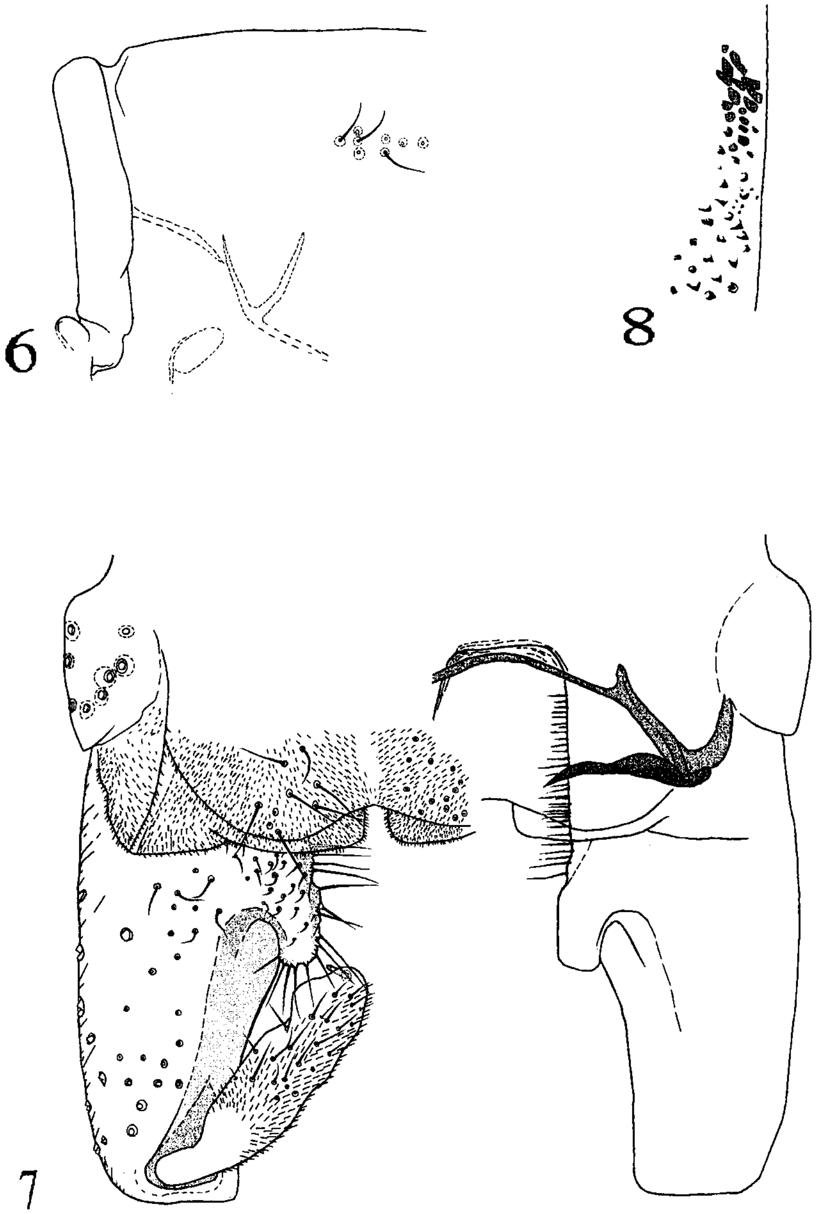
Genitalia (Fig. 7): Ninth tergum with 18 (2) setae. Gc/Gs ratio 1.80–1.81 (2).

PUPA (MALE).—Cephalothorax pale brown becoming dark brown posteriorly with a blackish spot over the base of each wing sheath. Abdomen yellowish brown becoming darker over the bases of the posterior tergal spine clusters; abdomen length 2.46–2.89 mm (3).

Cephalothorax: Setae absent on the frontal apotome, similar to that illustrated by Coffmann et al. (1986: Fig. 9.9A). Thoracic horn lacking. Median suture with strong tubercles on about middle 1/3 on either side; posteriorly the cephalothorax becomes rugose, then at extreme posterior end of the suture, fine, dark tubercles occur (Fig. 8). Precorneal setal cluster with 1 long (139 μm), 1 smaller (77 μm), and 1 very fine seta (62 μm). Dorsocentrals: Dc_1 coarse; Dc_2 smaller than, above, and slightly behind Dc_1; Dc_3 almost in a line with Dc_1 and about the same size; Dc_4 almost directly above Dc_3 and about the same size as Dc_2. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy (Fig. 9); tergum I with an anterior and posterior band of spines; terga II–VIII with bands of spinulae and spines similar to that illustrated for tergum V, but virtually devoid of shagreen between median spinulae band and posterior band of spines; anterior to the median band on T II–VIII, each tergum is covered with weak shagreen. Anal macrosetae with the anterior 1 well separated from the posterior 2 and either simple and spinelike or with weak apical or subapical bifurcations (Fig. 9); length 146 μm; length of longer posterior macroseta 149 μm; ALR 0.73–1.15; sternum VIII (Fig. 9).

DIAGNOSIS AND DISCUSSION.—The dark coloration and features of the male genitalia (Fig. 7) differentiate *C. platypus* from other Nearctic species of *Cardiocladius*. *Cardiocladius obscurus* (Johannsen) has similar coloration and genitalia; however, the basidorsal gonocoxite lobe of that species (Sublette 1967; Fig. 7) is more rounded, costa slightly extended, and scutellum pale. The pupa of *Cardiocladius obscurus* has been illustrated by Johannsen (1937) and Coffman et al. (1986: Fig. 9.9A, B) as *C.* cf. *obscuripes* (Johannsen) (sic! = *obscurus*). It differs from *C. platypus*, described herein, in 2 noticeable features: the apical spines on terga I–VIII are longer and more numerous, and shagreen is virtually lacking on terga II–VII between median and posterior bands of denticles. Further, the L-setae of T VIII are heavier than in the species illustrated by Coffmann et al. (1986).

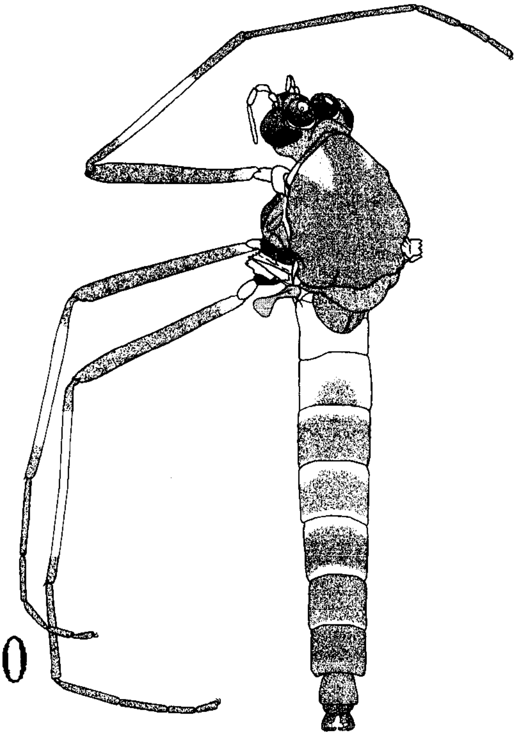


Figs. 6–8. *Cardiocladius platypus.* Male: 6, antepronotum, lateral view; 7, genitalia. Pupa: 8, cephalothoracic tubercles adjacent to median suture.

Pupae of the Palearctic species *C. fuscus* Kieffer and *C. capucinus* (Zetterstedt) differ among the features described and illustrated by Langton (1991).

ECOLOGY.—*Cardiocladius platypus* is an obligate, stenothermal rheophile that occurs throughout much of the upper Arkansas River in Colorado, with adults taken from 1497 to 3042 m elevation (Ruse et al. unpublished data). It has been taken in northern New Mexico (Sublette and Sublette 1979; unpublished records) in the Canadian, Rio Grande, and San Juan drainages. It occurs at stations with substrata ranging from rubble-gravel to gravel-sand.

DISTRIBUTION.—California to Colorado and New Mexico; Quebec (Oliver et al. 1990).



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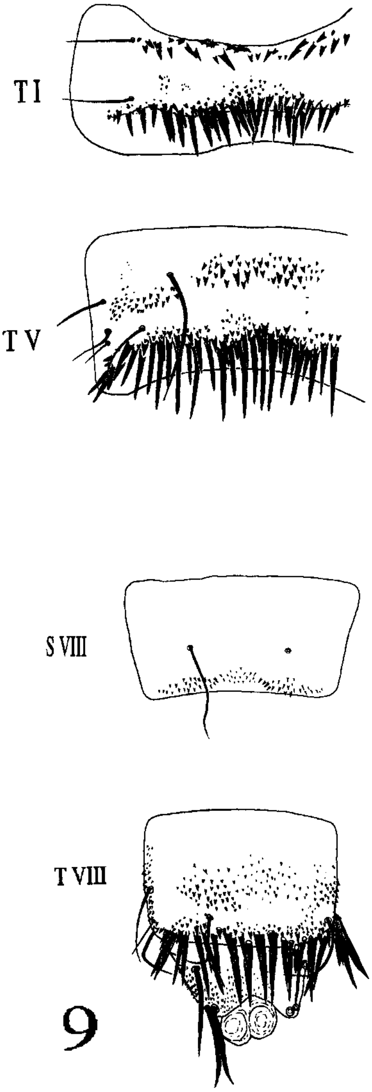

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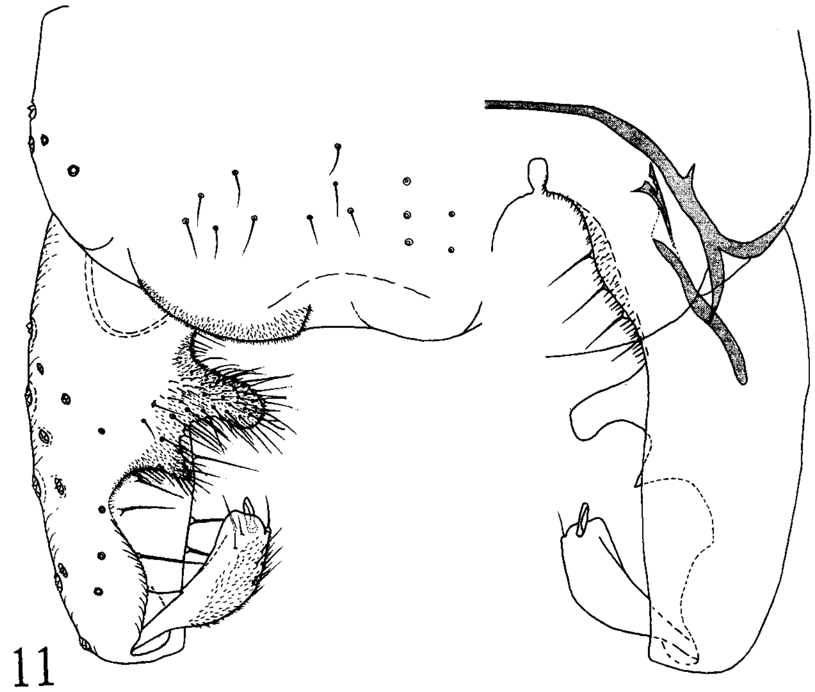
Figs. 9–10. *Cardiocladius platypus.* Pupa: 9, abdominal shagreen and chaetotaxy, terga I, V, VIII, anal lobe, and sternum VIII. *Cricotopus (Cricotopus) annulator.* Male: 10, coloration, semidiagrammatic.

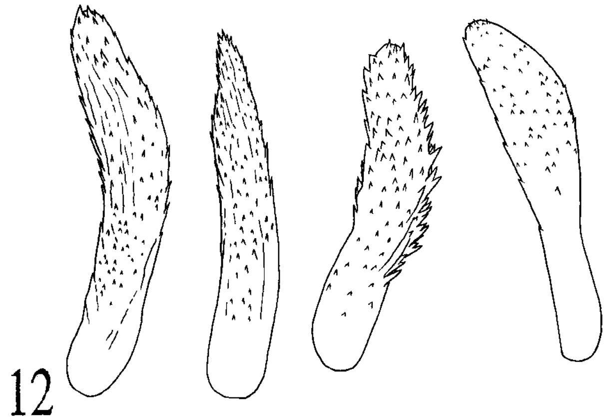
MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♀, river mi 0.0, 947 m elev; 1 ♂, river mi 72.0, 796 m elev; 1 ♂, river mi 108.0, 699 m elev; 1 ♂, 1 Pex, river mi 151.2, 556 m elev; 1 ♂, river mi 153.0, 549 m elev; 1 ♂, river mi 157.0, 555 m elev; 1 ♂, river mi 202.0, 457 m elev; 1 ♀ Pex, river mi 205.7, 451 m elev. Additional specimens examined from California, Colorado, and New Mexico.

Cricotopus (Cricotopus) annulator Goetghebuer

(Figs. 10–12)

Cricotopus annulator Goetghebuer 1927:52; type locality, Belgium.





Figs. 11–12. *Cricotopus (Cricotopus) annulator.* Male: 11, genitalia. Pupa: 12, thoracic horn variation.

Cricotopus irwini Sublette and Sublette 1971:97; type locality, California; male.

Cricotopus (Cricotopus) irwini Sublette & Sublette 1979:70, distribution, subgeneric position.

Cricotopus (Cricotopus) annulator Goetghebuer; Hirvenoja 1973:202, adults, immatures, distribution, synonymy; Laville 1979:160 and Rossaro 1987:333, ecology; LeSage and Harrison 1980a:73, adults, distribution, synonymy; 1980b:376, ecology; 1980c:2, biology of parasites; Simpson et al. 1983:4, adults, immatures, in key (after Hirvenoja 1973); Hudson et al. 1990:9, in list; Oliver et al. 1990:23; in catalog, synonymy; Langton 1991:219, pupa.

Cricotopus olivetus Boesel 1983:88; type locality, Ohio; male. *New synonym.*

The adult male and pupa differ slightly in some features from the description of Hirvenoja (1973). They are redescribed here to assist future comparisons.

MALE.—*Coloration* (Fig. 10): Head, fused thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum brown but usually paler than postnotum; humeral and pleural areas yellowish; legs dark with paler fasciae; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia yellowish at apex, somewhat infuscate basally.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.11–1.30 (4). Palpal proportions 55–70 (3):94–101 (3):117–133 (3):195–203 µm (3). Eyes with dorsal extension short and wedge-shaped. Ocular ratio 0.44–0.48 (3). Clypeus at base 0.86 of width of antennal pedicel; with 11–12 (4) setae. Temporal setae 7–10 (4), in a single row, reaching to near the midline of the head.

Thoracic chaetotaxy: Lateral antepronotals 5–8 (3); dorsocentrals 14–21 (7), in a partial double row; acrostichials 16–22 (7), mostly in 2 rows; prealars 5 (3); supra-alars lacking; scutellars 7–8 (3).

Wing: Membrane with microtrichia visible at 300X. Costa extended 54–60 µm (3) beyond R_{4+5}, which ends distal to M_{3+4} at 0.16 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.42–0.51 (3) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.09–1.14 (3). Wing length 1.80–1.97 mm (3). Squama with 8–9 (3) marginal setae. Wing vein setae R 6–9 (3); other veins without setae.

Legs: Foretibial spur length 44 µm (3). Middle tibial spur lengths 22–24/18–20 µm (3); hind tibial spur lengths 46–52/16–22 µm (3). Apical tarsomere, claws, empodium, and hyaline lamellae; pulvilli absent. Leg ratios: P I 0.59–0.65 (7); P II 0.47–0.50 (3); P III 0.56–0.59 (3). P III sensilla chaetica 6–7 (3).

Abdomen: Abdominal tergal setae: III, medians 5 (2), laterals 12–13 (2); IV, medians 5–7 (3), laterals 13–15 (2).

Genitalia (Fig. 11): Ninth tergum with 6–14 (3) setae. Gc/Gs ratio 2.48–2.69 (3).

PUPA.—Exuviae pale brown on posterior part of cephalothorax and darker brown on terga II–VI. Abdomen length 2.20–3.04 mm. *Cephalothorax*: Frontal setae absent on the frontal apotome. Thoracic horn variable in shape (Fig. 12), length 120–161 µm. Median suture with weak rugosity anteriorly on either side. Precorneal setae are of about equal length but with 1 slightly heavier. Dorsocentrals are small, almost in a straight line. Wing sheaths are without bacatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy similar to that figured in Hirvenoja (1973: Fig. 122-12). Tergum II hooks 43–65, in 2 rows; T II with a posterior row of fine shagreen just in front of hook row and in some specimens also a median band of very weak shagreen. Pedes spurii B (PSB) present on T II and T III, the latter being somewhat smaller and less projecting. Tergum VI with an oval to almost round median shagreen patch of which the L/W is 0.43–0.67. Anal macrosetae length 118–148 µm; anal lobe length 195–234 µm; ALR 0.61–0.63.

DIAGNOSIS AND DISCUSSION.—Abdominal and leg color patterns and genitalia of Nearctic specimens are so similar to the Palearctic species *C. (Cricotopus) annulator* that various authors have considered the 2 populations to be conspecific. Excellent reared material from Grand Canyon National Park and elsewhere clearly demonstrates some slight differences in the pupa from that described by Hirvenoja (1973) and Langton (1991). Most notable is the posterior shagreen band on T II as well as the presence of PSB on both T II and T III. The PSB on T III is, however, smaller than that on T II and, on some specimens, difficult to discern. A reexamination of the adults shows a slight difference in color bands of the foretibia as well as a genitalic difference in the basidorsal gonocoxite lobe, which is usually downturned at the apex.

ECOLOGY.—*Cricotopus annulator* inhabits flowing water systems ranging from spring runs to large rivers on a variety of substrata and under wide-ranging environmental conditions. Larvae usually concentrate in areas of moderate current with continuous adult emergence, but with spring and fall emergences accounting for about 90% of emergences at temperatures of 15–16°C. Adult males swarm at stream banks at less than 1 m height above clumps of grass (LeSage and Harrison 1980b). In Italy the species has been taken from *Typha latifolia* L. along the margin of a stream (Rossaro 1987). In England it was associated with *Sparganium* sp. and fine sediments in the River Pang (Ruse 1992), and *Myriophyllum spicatum* L. in a small stream, the River Tud (Tokeshi and Townsend 1987). Cobo and Gonzáles (1991) found it in relatively low numbers at 2 of 5 organically polluted sites on the River Sar in Spain. Schmid (1993) reported it in Austria in relatively low numbers among surface and gravel interstitial-dwelling larvae in a coldwater, gravel-bottomed stream. Similarly, Kownacki (1982) reported it to be relatively uncommon in a small pastureland stream in Poland. Anderwald et al. (1991) reported it from the Danube, a large river. In Germany, Kownacki and Margreiter-Kownacka (1993) found *C. annulator* in the soft sediments of the Alz River below a lake outflow as well as the firmer sediments of the lower stretches of the stream. Laville and Lavandier (1977) found this species at higher elevations in colder water over boulder-gravel substrata which had some moss and detritus in the French Pyrenees. In the Ossau Valley this species occurred at 500–2000 m elevation at maximum temperatures of 12–15°C (Laville and Vinçon 1991). In Lebanon, Moubayed and Laville (1983) reported *C. annulator* from the Beirut River at 700 m elevation, in slow to very slow summertime water flows, at a station with mosses in the current and macrophytes on the stream margins. Sublette and Sublette (1979) reported this species as being widely distributed in northern New Mexico streams, including the San Juan River, an upper tributary of the Colorado River. In the upper Arkansas River of Colorado it was taken at 1497–2743 m elevation on substrata that varied from boulder-cobble to gravel-sand (Ruse et al. unpublished data).

DISTRIBUTION.—This Holarctic species is widely distributed in the Nearctic region from California to Labrador.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 256 ♂♂ (some reared), 16 ♀♀ (some reared), 18 PP, throughout the river corridor from river mi 0.0, 947 m elev, to river mi 269.5, 356 m elev.

Cricotopus (Cricotopus) blinni
Sublette, new species

(Figs. 13–20, 54, 55)

HOLOTYPE MALE.—Grand Canyon National Park, Coconino Co., AZ, Colorado River mile 144.0, 570 m elev, 25-X-90, J.S., slide no. P0014 (CAS).

Coloration (Fig. 13): Head, thoracic vittae, scutellum, preepisternum, and postnotum blackish brown; antepronotum, humeral and pleural areas yellowish; legs dark with only trochanters and extreme base of all femora paler; abdomen fasciate, with T IV entirely yellowish and the genitalia dark.

Head (Fig. 54a): Antenna with 12 flagellomeres. Antennal ratio 1.02 (0.96–1.16; 11). Palpal proportions 47:86:117:148 μm (42–55:86–90: 109–117:148–187 μm; 6). Eyes with dorsal extension short and wedge-shaped; ocular ratio 0.43 (0.41–0.50; 6). Clypeus trapezoidal, about as wide at base as width of antennal pedicel; with 16 (8–16; 6) setae. Temporal setae 6 (6–8; 6), of which 2 (2–3; 6) are inner verticals near midline of the head, clearly separated from the 4 (4–6; 6) postoculars.

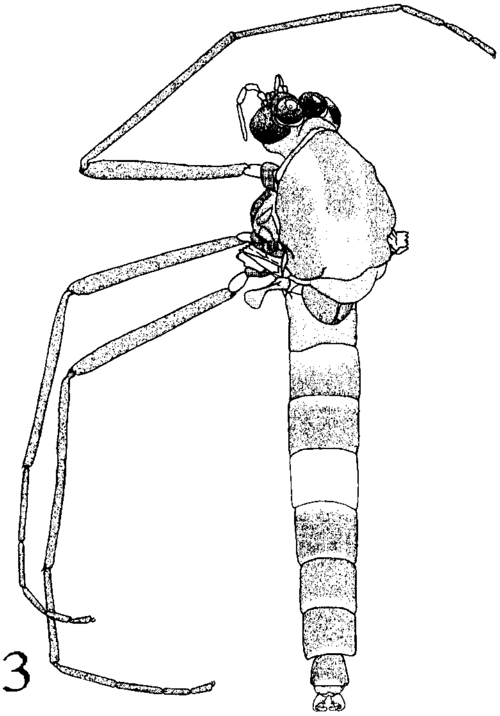
Thorax (Fig. 54a): Antepronotum almost parallel-sided near the dorsal apex. Thoracic chaetotaxy: lateral antepronotals 5 (5–9; 6); dorsocentrals 17 (11–25; 6), in a partial double row; acrostichials 18 (15–20; 6), mostly in 2 rows; prealars 4 (3–5; 6); supra-alars lacking; scutellars 17 (13–20; 6), in a strewn pattern.

Wing: Membrane with microtrichia visible at 300X. Costa extended 52 (13–56; 6) μm beyond R_{4+5}, which ends distal to M_{3+4} at 0.22 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.48 (0.51–0.59; 6) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.14 (1.11–1.21; 6). Wing length 1.94 (1.54–1.97; 6) mm. Squama with 5 (2–5; 6) marginal setae. Wing vein setae: R 4 (2–4; 5), R_{4+5} 0 (0–1; 6); other veins without setae.

Legs: Foretibial spur length 42 (36–44; 5) μm; middle tibial spur lengths 22/20 (24–26/ 22–26; 5) μm; hind tibial spur lengths 56/24 (46–60/20–28; 5) μm. Apex of tarsomere 5, claws, hyaline lamellae, empodium and ungitractor (Fig. 54e), pulvilli vestigial. Leg ratios: P I 0.59 (0.58–0.62; 5); P II 0.44 (0.45–0.48; 5); P III 0.57 (0.53–0.58; 5). P III comb setae 14 (12–17; 5). P III sensilla chaetica 6 (5–9; 5).

Abdomen: Tergal setal pattern T II–T IV (Fig. 14); setae: III, medians 4 (4–7; 5), laterals 13 (9–13; 5); IV, medians 4 (4–6; 5), laterals 11 (7–19; 5).

Genitalia (Figs. 15, 54c): Ninth tergum with 13 (10–14; 5) setae. Gc/Gs ratio 2.0 (2.03–2.24; 5). Slide mounts of this (and other) species show much variation in the gonostylus, depending on the orientation; Figures 54f–h show the appearance of the gonostylus in various rotational positions. Apex of basidorsal gonocoxite lobe without dorsal microtrichia (Fig. 54c).



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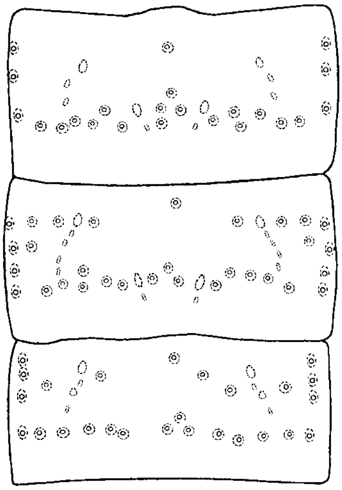

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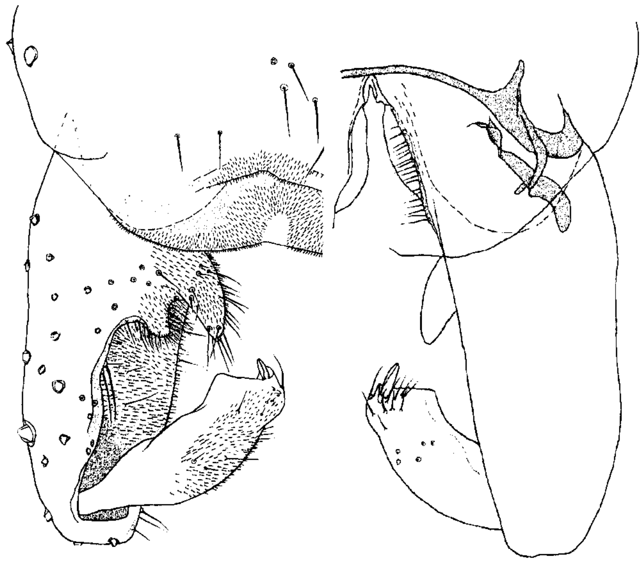

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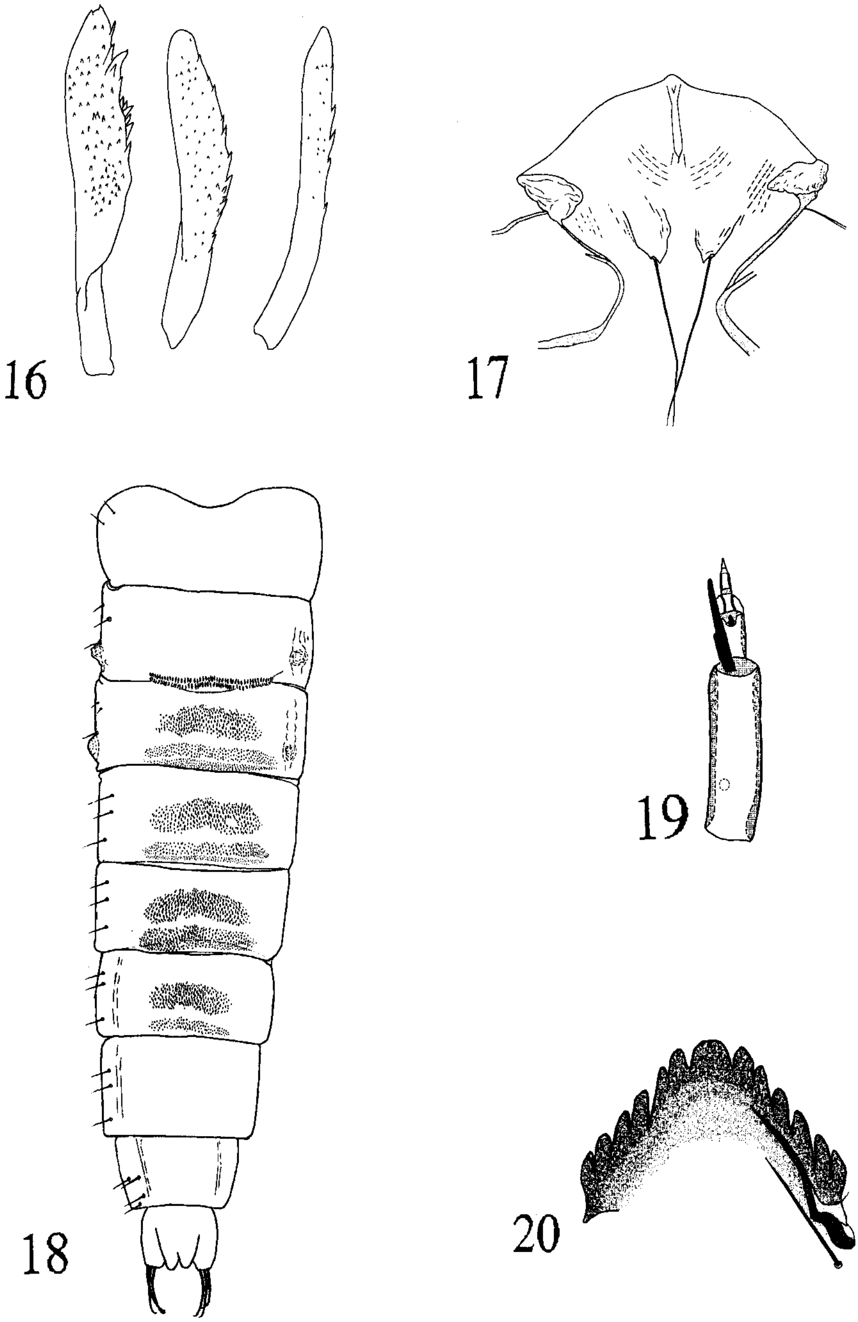
Figs. 13–15. *Cricotopus (Cricotopus) blinni.* Male: 13, coloration, semidiagrammatic; 14, terga II–IV, chaetotaxy; 15, genitalia.



Figs. 16–20. *Cricotopus (Cricotopus) blinni.* Pupa: 16, thoracic horn variation; 17, frontal apotome; 18, abdominal shagreen and chaetotaxy. Larva: 19, antenna; 20, mentum.

PUPA.—Abdomen length 2.04–2.65; 2.36 mm (6). *Cephalothorax*: Cephalothorax pale brown. Frontal setae present on the frontal apotome (Fig. 17); frontal setal length 86–152 µm (2). Thoracic horn variation (Fig. 16), length 170–226; 189 µm (6). Median suture of cephalothorax with strong rugosity on either side; lateral surface of cephalothorax with weak, scale-like tubercles. Precorneal setae subequal in length with 1 very slightly weaker than the other 2. Dorsocentrals small, almost in a line. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdominal terga I–VI pale brown. Shagreen pattern and chaetotaxy (Fig. 18); details of shagreen on tergum III (Fig. 54b). Tergum II hooks 59–84; 66 (7), in 2 rows (Fig. 54d). Pedes spurii B present on terga II and III. Anal lobe length 198–201 µm (4); anal macrosetae length 130–155; 145 µm (4). ALR 0.73–0.80; 0.77 (4).

LARVA.—Ventral head length 164–187 µm (3). Head entirely pale except for darkened occipital ring, tips of the mandible, and mentum.

Antenna (Fig. 19): Blade shorter than flagellum; lauterborn organs large, extending to apex of 3rd segment; ring organ at 0.23 from the base.

Epipharyngeal region (Fig. 55b): S I apically bifurcate; pecten epipharyngis of 3 unequal blades which are apparently fused (Fig. 55b); chaetae 5; spinulae about 3; chaetulae laterales 7, variable in size and shape; chaetulae basales 2, weakly dissected apically. Ungula V-shaped with the basal sclerite quadrangular. Premandible with 1 apical tooth and a slight subapical shelf; brush lacking.

Maxilla (Fig. 55e): Lacinial chaetulae 5; antaxial seta shorter than lacinial chaetulae; paraxial seta shorter than antaxial seta; palpus with 13 sensillar structures (Fig. 55d).

Mandible (Fig. 55a): Apical tooth shorter than combined width of the 3 inner teeth; seta subdentalis apically pointed; seta interna (not shown) with 3 main branches which are simple; outer margin moderately crenulate; mola smooth.

Mentum (Fig. 20): Median tooth <2X width of 1st laterals; 2nd lateral slightly shorter than 1st and 3rd. Anterior parapods pectinate (Fig. 55c), with claws progressively diminishing in size posteroventrally.

DIAGNOSIS AND DISCUSSION.—The genitalia and chaetotaxy resemble those of the *festivellus*-group (Hirvenoja 1973), but members of that group have P II sensilla chaetica which are lacking in this species; also the abdominal color pattern of this species is distinctively different. It also closely resembles *C. (Cricotopus) herrmanni* Sublette, new species, in genitalic features and abdominal chaetotaxy, but that species has a significantly lower antennal ratio and a strikingly different color pattern. The larva is also similar to members of the *festivellus*-group, but the central tooth of the mentum is much narrower than in known members of that group. The pupa is similar to the Palearctic species *C. albiforceps* Kieffer (Hirvenoja 1973: Fig. 140), but that species has pedes spurii B only on tergum II, while this species has both PSB II and III. Also, the thoracic horn appears to be less spinose. The pupa is very similar to that of *C. (Cricotopus) herrmanni* Sublette; however, the length of the thoracic horn is usually less than that of *C. herrmanni*, and the anal macrosetae are shorter than 125 µm.

ECOLOGY.—This species is widely distributed in the cold, swift Colorado River corridor, with specimens collected from Lees Ferry to mile 166.5. Adults were collected from July to February.

DISTRIBUTION.—California to Colorado and New Mexico.

PARATYPES.—AZ: 2 ♂♂, collected with the holotype (NAU). Mohave Co., 1 ♂, Colorado R, Bullhead City, 5-IX-73, M.S. Mulla (UCR). Coconino Co., 1 L, Colorado R, Grand Canyon National Park, river mi 0.5, 950 m elev; 2 ♂♂, river mi 133.0, 597 m elev; 1 ♀, river mi 133.5, 600 m elev; 1 ♂, river mi 144.0, 572 m elev; 1 ♂, river mi 166.5, 532 m elev.

CA: Riverside Co., 3 ♂♂, Laflin Ranch, between Thermal and Mecca, 15-V-70, lt. tr. (UCR); San Bernardino Co., 7 ♂♂, Spring Valley L, 11-IX-73, M.S. Mulla (UCR, JES).

CO: Lake Co., 1 ♂, 4 ♀♀, E fork of Arkansas R, 3042 m elev, 20–21-IX-84, S.J. Herrmann. Pueblo Co., 69 ♂♂, Arkansas R, Pueblo Blvd Br, 1431 m elev, 31-X–1-XI-84, 4-XI-84, S.J. Herrmann; 9 ♂♂, 22-VIII-83, P. Sanchez; 70 ♂♂, Stilling Basin Br, below Pueblo Res, 1444 m elev, 10-VI-85, 15-VIII-85, 18-IX-85, 17-VII-87, S.J. Herrmann; 6 ♂♂, Hobson Ranch, 1504 m elev, 19-IX-85, 17-VII-87, S.J. Herrmann. Fremont Co., 10 ♂♂, Portland Br, 1535 m elev, 21-III-85, 19-IX-85 (SJH, JES, UC, KU, ANSP, CAS, AEI, CNC, USNM, INHS, UMN, BYU).

NM: Santa Fe Co., 22 ♂♂, Rio Grande, Otowai Br, near San Ildefonso Pueblo, 8-IX-74, 5-X-74, 16-VII-76, malaise trap, sweep net, M. Beard (JES). Socorro Co., 1 ♂, Rio Grande, nr San Marcial, 11-VII-76, sweep net, M. Beard. Doña Ana Co., 6 ♂♂, Rio Grande, at Texas state line, 15-XI-74, M. Beard. Catron Co., 8 ♂♂, 1 ♀, San Francisco R, south of Pleasanton, nr Frisco Hot Spgs, 10-VII-74, 17-IX-74, malaise trap, 18–24-XI-74 (reared), M. Beard (JES). Quay Co., 4 ♂♂, Canadian R, at mouth of Revelto Cr, 1-X-74, M. Beard. Colfax Co., 3 ♂♂, Canadian R, Hwy 54, at Taylor Spgs, 3-X-74, sweep net, M. Beard. San Juan Co., 1 ♂, San Juan R, 1 mi W San Juan Co. Hospital, 18-VII-76, M. Beard, J.E. Sublette (JES).

This species is dedicated to Dr. Dean W. Blinn, limnologist at Northern Arizona University, Flagstaff, for his assistance in bringing this project to fruition.

Cricotopus (Cricotopus) globistylus Roback

(Figs. 21–32, 56)

Cricotopus globistylus Roback 1957:10, male and female, type locality, Heber-Midway bridge, Wasatch Co., Utah; Sublette and Sublette 1979:69, in list; Oliver et al. 1990:25, catalog.

The male has been very briefly described and inadequately illustrated (Roback 1957). The following is a more complete description of the male together with descriptions of the pupa and larva.

MALE.—*Coloration* (Fig. 21): Head, thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum paler than postnotum; humeral and pleural areas yellowish; legs dark; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia dark.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.63–1.17; 0.82 (17). Palpal proportions 39–78:86–140:86–117:125–164 µm. Eyes with dorsal extension short, wedge-shaped. Ocular ratio 0.44–0.53 (3). Clypeus quadrangular, slightly wider at base than width of antennal pedicel; with 6–19 (15) setae. Temporal setae 10–13 (6), in a slightly staggered single row, reaching near midline of head.

Thorax: Antepronotum moderately produced at dorsal apex (Figs. 22, 56a). Thoracic chaetotaxy: lateral antepronotals 8–14; 11 (5); dorsocentrals rather coarse, 17–25 (6), in a partial double row (Fig. 56a); acrostichials 10–18 (6), mostly in 2 rows; prealars 3–7 (6); supra-alars absent; scutellars 21–38 (6), in a strewn pattern.

Wing: Membrane with microtrichia visible at 300X. Costa extended 28–50 µm beyond R_{4+5}, which ends distal to M_{3+4} at 0.39 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.34–0.45 (6) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.0–1.05 (6). Wing length 1.47–2.23 (6) mm. Squama with 4–10 (6) marginal setae. Wing vein setae: R 6–14 (6); other veins without setae.

Legs: Foretibial spur length 48–71 (6) µm; middle tibial spur lengths 31–37/20–30 (6) µm; hind tibial spur lengths 56–74/22–36 (6) µm. Pulvilli absent. Leg ratios: P I 0.53–0.57 (6); P II 0.37–0.44 (6); P III 0.46–0.53 (6). P III comb setae 7–13 (6). P III sensilla chaetica 5–10 (6).

Abdomen: Abdominal tergal setae (Fig. 23): T III, medians 5–13 (6), laterals 11–22 (6); T IV, medians 8–13 (6), laterals 12–27 (6).

Genitalia (Fig. 24): Ninth tergum with 5–16 (6) setae. Gc/Gs ratio 2.31–2.48 (6).

PUPA.—Exuviae pale brown except for darker brown shagreen patches. Abdomen length 2.65–3.08 mm (5).

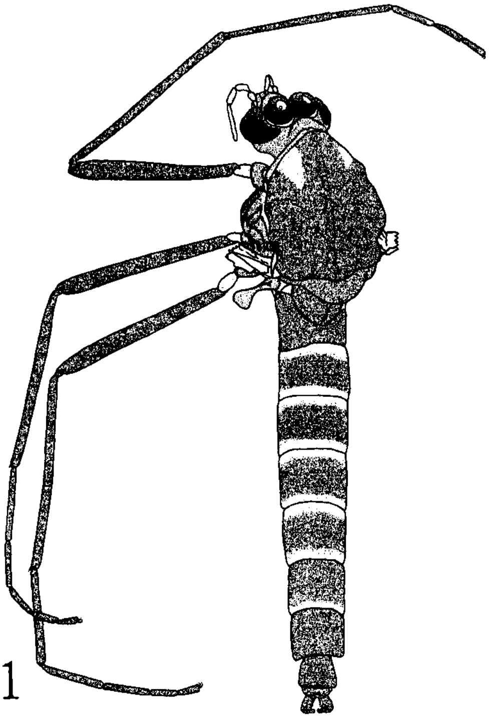
Cephalothorax: Frontal setae present but frequently lost. Thoracic horn (Fig. 25), length 88–108 µm (5). Median suture with weak rugosity on either side. Precorneal setae with 1 long and 2 slightly smaller setae. Dorsal antepronotal seta much longer than ventral. Dorsocentrals small, almost in a line. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Shagreen pattern and chaetotaxy (Figs. 26, 56b–d). Tergum II hooks 57–72 (5), in 2 rows (Figs. 26, 56e,f); anterior to the hook row is a weak band of fine shagreen, which is occasionally absent. Pedes spurii B present on tergum II, broad and poorly defined. Pedes spurii A present on terga III–VI. Anal macrosetae length 125–127 (5) µm, heavy and only weakly curved at the tip, occasionally bifurcate; ALR 0.43–0.59 (5). Tergum VIII with 5 L-setae or occasionally with 4 only (as shown in Fig. 26).

LARVA.—Ventral head length 257 µm. Head pale brown with posterolateral margin dark, as are the occipital ring and tips of the mandible and mentum.

Antenna: With 5 segments (Fig. 27); length 99 µm; blade shorter than the flagellum, extending to level of 3rd segment; lauterborn organs moderately large but not reaching apex of 3rd segment; ring organ at 0.29 from base of 1st segment.

Epipharyngeal structures (Fig. 28): S I apically bifurcate; pecten epipharyngis of 3 unequal blades; chaetae 8; spinulae 5; chaetulae laterales 6; chaetulae basales 2, weakly fimbriate apically; ungula V-shaped with basal sclerite quadrangular. Premandible with 1 apical tooth; brush lacking.



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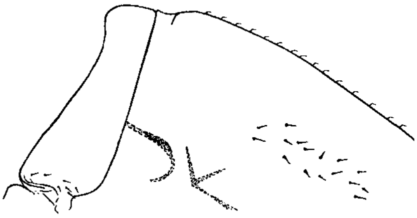

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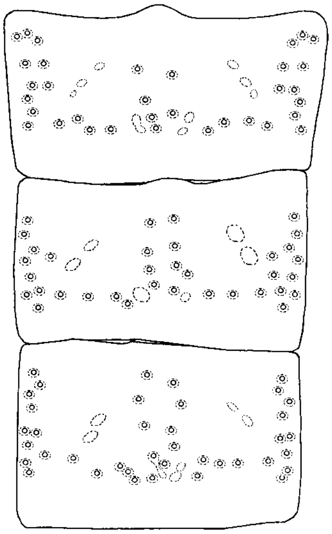

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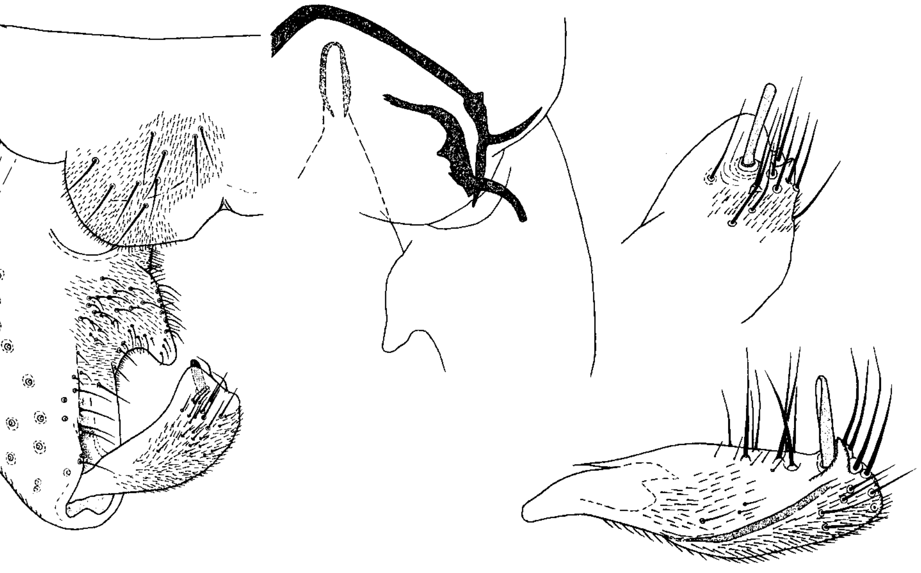

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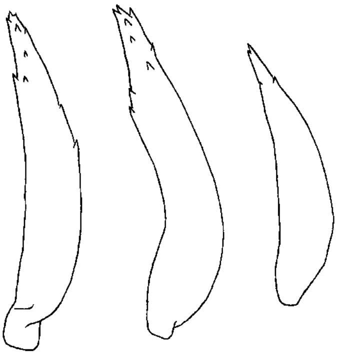
Figs. 21–24. *Cricotopus (Cricotopus) globistylus.* Male: 21, coloration, semidiagrammatic; 22, antepronotum, lateral view; 23, terga II–V chaetotaxy; 24, genitalia (left, dorsal; middle, internal skeleton; right, 2 views of gonostylar apex).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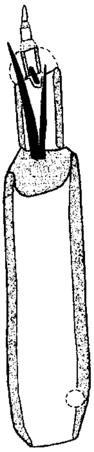
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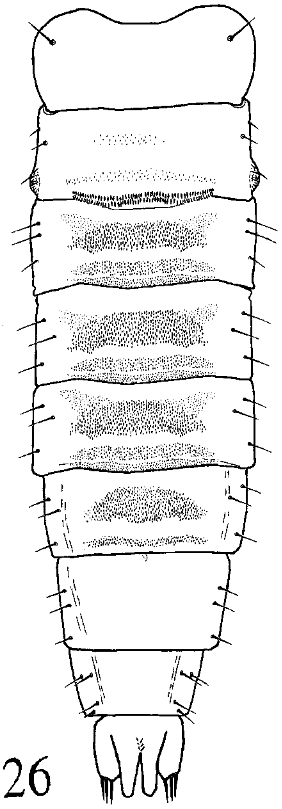
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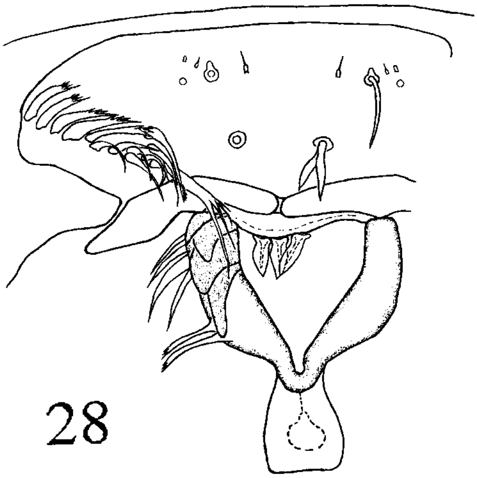
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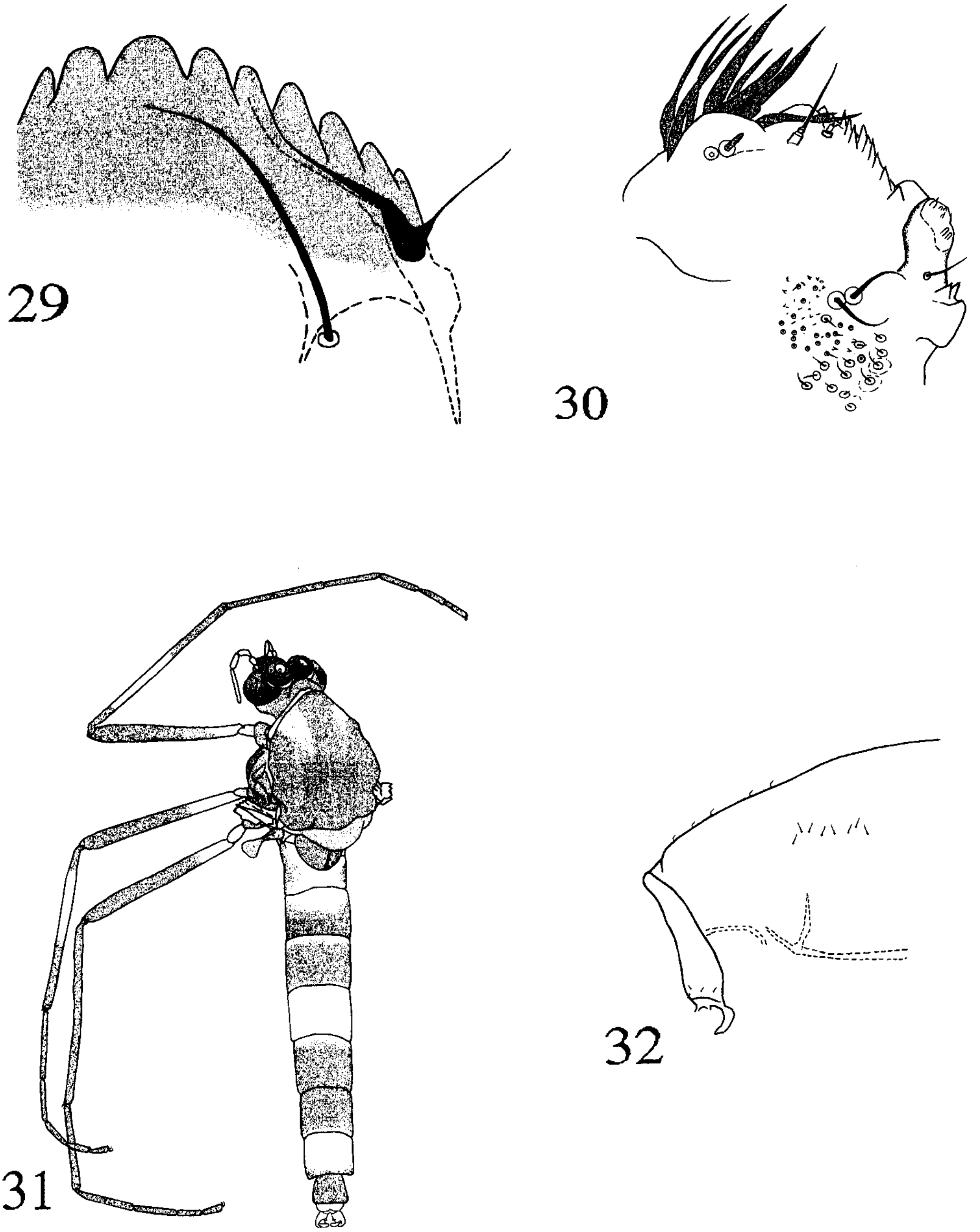
Figs. 25–28. *Cricotopus (Cricotopus) globistylus.* Pupa: 25, thoracic horn variation; 26, abdominal shagreen and chaetotaxy. Larva: 27, antenna; 28, epipharyngeal structures.

Mandible: Apical tooth shorter than combined width of 3 inner teeth; seta subdentalis apically notched; seta interna not discernible; outer margin strongly crenulate; mola smooth.

Mentum (Fig. 29): One median tooth which is <2X 1st laterals that are larger than remainder, which diminish in size laterally.

Maxilla (Fig. 30): Lacinial chaetae with 6 large anterior and about 4 smaller posterior blades; palpi slightly longer than wide.



Figs. 29–32. *Cricotopus (Cricotopus) globistylus.* Larva: 29, mentum; 30, maxilla. *Cricotopus (Cricotopus) herrmanni.* Male: 31, coloration, semidiagrammatic; 32, anteprontum, lateral view.

Body: With abdominal hair clusters of 1–4 setae up to 189 μm long; procercus dark brown, about as wide as high, with 1 long and 1 short setae on posterior face and 6 long terminal setae; each posterior parapod with about 13 yellowish brown claws.

DIAGNOSIS AND DISCUSSION.—The abdominal chaetotaxy, massive gonostylus, and fused basiventral and basidorsal lobes of the gonocoxite distinguish the male of this species from all other Holarctic *Cricotopus*. In Hirvenoja (1973) *C. globistylus* keys to the *fuscus*-group;

however, in that group the basidorsal and basiventral lobes are more or less separated and no species has such a massive gonostylus. The pupa, which lacks frontal setae, a scarcely discernible PSB on T II, a small, weakly spinose thoracic horn, shagreen patches on T III–VI well separated, and a weak L-seta on T VIII, does not fit any of Hirvenoja's groups. The larva, which has a central tooth of the mentum that is less than twice the width of the 1st laterals, also does not fit any of Hirvenoja's groups.

ECOLOGY.—This species occurs most often in cold streams with gravel bottoms. In Grand Canyon it is most common in the uppermost, clearwater reach above the Paria River confluence.

DISTRIBUTION.—Known from California north to Oregon and east to Montana and New Mexico.

MATERIAL EXAMINED: AZ: Coconino Co., Grand Canyon National Park, Colorado River, 74 ♂♂ (some reared), 8 ♀♀ (some reared), 27 Pex, river mi 0.0, 947 m elev, to river mi 109.0, 710 m elev. UT: Paratype ♂, Wasatch Co., Heber-Midway Br, 26-XI-54, Gerald D. Brooks (ANSP). Also, specimens, including reared material, from California, Oregon, Idaho, Montana, and New Mexico (CAS, USNM, JES).

Cricotopus (Cricotopus) herrmanni Sublette, new species

(Figs. 33–35, 57)

HOLOTYPE MALE.—Arkansas River, Fremont Co., CO, Canyon City, 9th street bridge, T85S, R70W, S33, 1618 m elev, 19-IX-85, S.J. Herrmann (CAS).

Coloration (Fig. 31): Head, thoracic vittae, preepisternum, scutellum, and postnotum blackish brown; antepronotum, humeral and pleural areas yellowish; legs dark with paler fasciae; abdomen fasciate, with dark brown bands interspersed with yellowish bands; genitalia yellowish at apex, somewhat infuscate basally.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.58 (0.40–0.62; 12). Palpal proportions 47 (47–62; 6):86 (78–94; 6):109 (101–117; 6):[terminal palpomere on holotype shriveled] (156–211; 6) µm. Eyes with dorsal extension short and wedge-shaped. Ocular ratio 0.43 (0.40–0.46; 6). Clypeus quadrangular, slightly narrower at base than width of the antennal pedicel; with 8 (7–11; 6) setae. Temporal setae 9 (6–9; 6), of which 4 are inner verticals near the midline of the head widely separated from the remainder.

Thorax: Antepronotum almost parallel-sided in apical half (Fig. 32). Thoracic chaetotaxy: lateral antepronotals 6 (3–6; 6); dorsocentrals 18 (13–19; 6), in a partial double row, with the posterior setae distinctly coarser than the anterior; acrostichials 15 (14–21; 6), partially in 2 rows; prealars 4 (3–5; 6); supra-alars lacking; scutellars 15 (16–21; 6), irregularly biserial laterally becoming uniserial towards the middle, but with a median gap.

Wing: Membrane with microtrichia visible at 300X. Costa extended 60 (48–70; 6) µm beyond R_{4+5}, which ends distal to M_{3+4} at 0.26 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} ends at 0.56 of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.24 (1.14–1.20; 6). Wing length 1.68 (1.52–1.90; 6) mm. Squama with 4 (3–5; 6) marginal setae. Wing vein setae: R 3 (3–5; 6), other veins without setae.

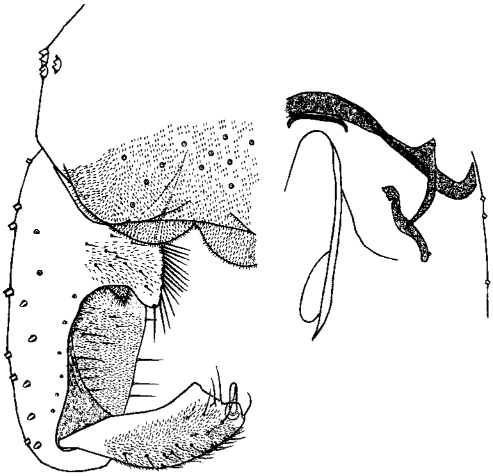
Legs: Foretibial spur length 44 (32–50; 6) µm; middle tibial spur lengths 26/24 (20–28/14–24; 5) µm; hind tibial spur lengths 58/26 (44–60/20–30; 6) µm. Pulvillus vestigial but hyaline lamella and empodium well developed. Leg ratios: PI 0.59 (0.58–0.64; 6); P II 0.47 (0.44–0.47; 6); P III 0.58 (0.51–0.59; 6). P III comb setae 13 (12–16; 6), with tips of the comb setae forming an arc. P III sensilla chaetica 7 (6–10; 7).

Abdomen: Abdominal tergal setae: T III, medians 6 (4–8; 6), laterals 10 (8–12; 6); T IV, medians 4 (4–7; 6), laterals 10 (5–13; 6); setal pattern similar to *C. blinni*, n. sp.

Genitalia (Figs. 33, 57a): Ninth tergum with 10 (11–22; 6) setae. Gc/Gs ratio 2.22 (2.04–2.40; 6). As in other species of *Cricotopus*, the gonostylus shows considerable variation in appearance due to position at the time of slide mounting; Figures 57b–d illustrate some of the variation observed at various angles due to slide-mounting differences.

PUPA.—*Exuviae*: Almost entirely pale brown; tergum VI still darker brown.

Cephalothorax: Frontal setae 60–70 µm (2). Thoracic horn (Fig. 34), length 214–275; 252 µm (7). Median suture with moderate rugosity on either side; lateral surface with weak, scale-like tubercles. Precorneal setae, 2 large, 1 slightly smaller. Dorsocentrals small, almost in



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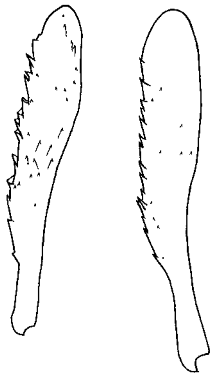

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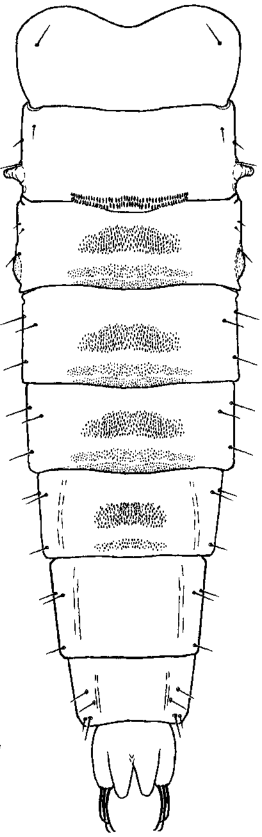

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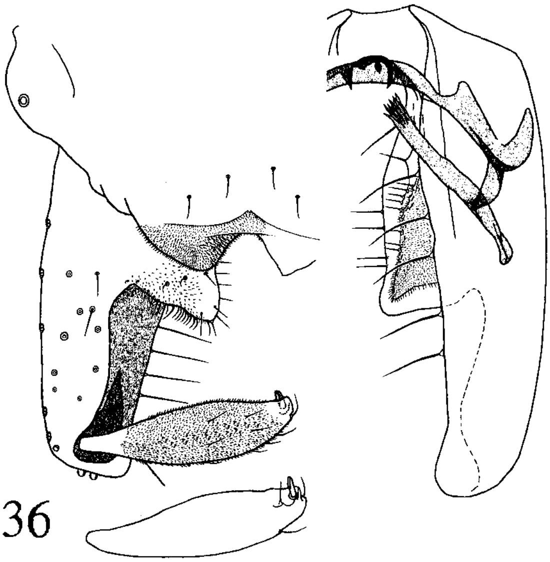


36

Figs. 33–36. *Cricotopus (Cricotopus) herrmanni.* Male: 33, genitalia. Pupa: 34, thoracic horn variation; 35, abdominal shagreen and chaetotaxy. *Eukiefferiella ilkleyensis.* Male: 36, genitalia.

a straight row. Wing sheath without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen length 2.42–2.89 mm (5). Shagreen pattern and chaetotaxy (Fig. 35). Tergum II with 67–82; 71 (5) hooks in 2 very regular rows. Pedes spurii B present on terga II and III, with the PSB on II large and projecting and that on III smaller and rounded. Width of medial shagreen band on T III less than posterior. Medial shagreen of T VI L/W 0.31–0.37 (3). Anal lobe length 195–234; 214 µm (7). Anal macrosetae length 156–172; 162 µm (7). ALR 0.0.69–0.83; 0.76 (7).

Diagnosis and discussion.—The adult can be clearly differentiated from *C. blinni* by the distinctively different coloration (cf. Figs. 13, 31). The genitalia are very similar to those of *C. blinni* as well as members of the *cylindraceus*-group and *festivellus*-group (Hirvenoja 1973); however, these 2 groups differ in color. The pupa is very similar to that of *C. blinni*, but it has a slightly longer thoracic horn and longer anal macrosetae.

Ecology.—This species has been collected most frequently from coldwater streams with gravel-sand substrata.

Distribution.—California to Colorado and New Mexico.

Paratypes and material examined.—AZ: Coconino Co., 1 ♂, Grand Canyon National Park, Colorado R, river mi 31.0, 876 m elev; 4 ♂♂, river mi 31.8, 876 m elev; 2 ♂♂, river mi 133.0, 597 m elev. Cochise Co., 1 ♂, Southwestern Research Station, 1646 m elev, V. Roth (UCR).

CA: 1 ♂, Davis, R.O. Schuster (UCD); 1 ♂, Hopeland, E.P. Van Duzee (CAS); 1 ♂, Oakland, E.S. Rosa (CAS); 1 ♂, Tule R, Springville, W.W. Wirth (USNM); 1 ♂, Whitewater, A.L. Melander (USNM). Alameda Co., 1 ♂, Sunol, W.W. Wirth (USNM). Inyo Co., 1 ♂, Surprise Canyon, R.O. Schuster (CIS). Nevada Co., 1 ♂, Sagehen Cr, nr Hobart Mills, C.N. Slobodchikoff (CAS). Riverside Co., 3 ♂♂, P.L. Boyd Desert Research Center, Saul I. Frommer, L. LePre; 1 ♂, Horsethief Cr, 10 mi S Palm Desert, L. LaPre; 1 ♂, Desert Hot Springs (UCR); 1 ♂, 1000 Palms Canyon, P.A. Rausch (UCR). San Bernardino Co., 1 ♂, Mill Cr, Thurman Flats, P.A. Rausch (UCR). Santa Clara Co., 2 ♂♂, Coyote Creek, R. Whitsel (JES). Shasta Co., 118 ♂♂, Fall River Mills; 1 ♂, Hat Creek, Pitt R, C. Apperson (BYU, CAS, INHS, KU, JES, UCR, USNM). Sonoma Co., 1 ♂, Triniti, N.W. Frazier (CAS). Tenama Co., 2 ♂♂, Red Bluff (CAS). Tulare Co., 1 ♂, E Success Res, T.W. Fisher (UCR).

CO: Chaffee Co., 18 ♂♂, Arkansas R, Rd 301, Fisherman's Br, 2338 m elev, T15S, R78W, S3; 40 ♂♂, 6 ♀♀, Sand Lake Br, Salida, 2143 m elev, T50N, R9E, S31, Chalk Cr; 1 ♂, Hwy 285, 2338 m elev, T15S, R77W, S14. Fremont Co., 12 ♂♂, 1 P & ♂, Arkansas R, Howard Br, 2033 m elev; 22 ♂♂, Parkdale Siding Br, 1747 m elev, T18S, R72W, S13; 17 ♂♂, Hwy 115, 9th St Br, Canyon City, 1618 m elev, T85S, R70W, S33; 9 ♂♂, Texas Cr Br, 1879 m elev, T19S, R73W, S7; 21 ♂♂, Portland Br, 1535 m elev, T19S, R68W, S17/20. Lake Co., 1 ♂, Arkansas R, upstream from Lake Cr inflow, 2748 m elev, T11S, R80W, S24. Pueblo Co., 1 ♂, Arkansas R, Hobson Ranch, 1504 m elev, T20S, R67W, S6; 6 ♂♂, Stilling Basin Br, 1444 masl, T20S, R66W, S36, all (except as indicated) collected by S.J. Herrmann (AEI, CAS, JES, UMN, USNM).

NM: Rio Arriba Co., 1 ♂, Chama R, 2 mi S Chama, Doles and Milensky; 1 ♂, Chama R below El Vado Dam, Doles and Milensky (JES).

This species is dedicated to Dr. Scott J. Herrmann, University of Southern Colorado, who collected a significant part of the type series from the Arkansas River in Colorado.

Cricotopus (Cricotopus) infuscatus (Malloch)

Orthocladius infuscatus Malloch 1915:517; type locality, Peoria, IL.

Cricotopus (Cricotopus) infuscatus (Malloch); Sublette and Sublette 1979:69, distribution, synonymy; LeSage and Harrison 1980a:81 and Fig. 10, adults, immatures, distribution; 1980b:376, ecology; 1980c:2, biology of parasites; Oliver et al. 1990:23, catalog, synonymy.

Cricotopus edurus Sublette & Sublette 1971:85; type locality, P.L. Boyd Desert Research Center, near Palm Desert, Riverside Co., CA. *New synonym.*

Cricotopus subfuscus Sublette & Sublette 1971:98; type locality, Hat Creek, Fall River Mills, Shasta Co., CA. *New synonym.*

Cricotopus infuscatus (Malloch); Boesel 1983:83, distribution, synonymy.

Diagnosis.—The sharply defined basidorsal and basiventral lobes of the gonocoxite which are about of equal length, the basidorsal lobe which bears about 6–8 main setae (Sublette and Sublette 1971: Figs. 6, 35; LeSage and Harrison 1980a: Fig. 10), and the abdominal chaetotaxy (Sublette and Sublette 1971: Figs. 5, 34), together with the color pattern (Sublette and Sublette 1971: Figs. 1, 2), separate this species from other Nearctic *Cricotopus*. The larva and pupa have been characterized by LeSage and Harrison (1980a:84); both stages are similar to those of *C. (Cricotopus) annulator* (Goetghebuer), described above. The pupa differs in usually lacking the apical shagreen band on T II and having a higher number of recurved hooks on T II (63–112). The number of recurved hooks on T II is quite variable, with eastern populations generally having a higher number. The larva has a strongly crenulate mandible, which is in contrast to that of *C. annulator* with its virtually smooth outer mandibular margin.

DISCUSSION.—Additional material of *C. infuscatus* indicates a much broader range of color variation and chaetotaxy than was previously known, hence the synonymies given above.

ECOLOGY.—Lenat and Folley (1983) demonstrated a bimodal pattern of adult emergence for adults in the *infuscatus*-group. LeSage and Harrison (1980b) reported that *C. infuscatus* could tolerate pollution, 80% of the populations occurred in riffles, most emergences were at temperatures of 16–21°C, and swarming occurred over grass clumps or the ground at less than 1 m in height at 7–11 m from the stream margin. Ruse et al. (unpublished data) collected adults from the upper Arkansas River in Colorado at elevations ranging from 1431 to 2748 m.

DISTRIBUTION.—Widely dispersed throughout lower elevations and latitudes of North America.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 3 ♂♂, river mi 61.5, 826 m elev; 1 ♂, river mi 63.7, 818 m elev; 1 ♂, river mi 164.5, 533 m elev; 2 ♂♂, river mi 166.5, 532 m elev. Other material: Adults have been examined from throughout most of the range of this species in North America, including extensive reared series from South Dakota and New Mexico.

Cricotopus (Cricotopus) *trifascia* Edwards

Cricotopus trifascia Edwards 1929:322, male. Type locality, England; Boesel 1983:84, distribution.

Cricotopus (Cricotopus) trifascia Edwards; Hirvenoja 1973:244, adults, pupa, larva, review, distribution; Sublette and Sublette 1979:70; synonymy, distribution; Laville 1979:160 and Wilson 1987:391, ecology; LeSage and Harrison 1980a:102, distribution, synonymy; 1980b:376, ecology; 1980c:2, biology of parasites; Lenat and Folley 1983:152, phenology, distribution; Mason and Lehmkuhl 1983:196, 1985:877, distribution, phenology; Simpson et al. 1983:4, distribution, adults, pupa, larva, in key (after Hirvenoja 1973); Hudson et al. 1990:9, in list, distribution; Oliver et al. 1990:24, distribution, synonymy; Langton 1991:208, pupa.

DIAGNOSIS AND DISCUSSION.—This is the only Nearctic species of *Cricotopus* that lacks a basidorsal gonocoxite lobe. The pupa has the distinctive features of heavy shagreen on terga VII and VIII as well as 2 large and 1 small macrosetae on the anal lobe.

ECOLOGY.—*Cricotopus trifascia* is usually in rapidly flowing waters ranging from 1st-order streams to large rivers (Simpson and Bode 1980). In small streams in England it has been taken on gravel or *Ranunculus* (Pinder 1980, Pinder and Farr 1987). Mason and Lehmkuhl (1983) reported 3 peaks of adult emergence upstream from an impoundment: spring, midsummer, and fall. However, highest numbers were found 23 km downstream from the impoundment and with a unimodal, midsummer emergence about a month after the upstream populations. In Germany, Kownacki and Margreiter-Kownacka (1993) reported *C. trifascia* as occurring more commonly in the lower stretches of the Alz River rather than immediately below a lake outflow; in the Fulda, Lehmann (1971) found this species rather widely distributed, occurring in the metarhithral to the potomal regions in moderately strong current. The species was the dominant form in a small, heavily polluted stream in southern Ontario, absent from another polluted stream, but clearly rheophilous with at least 80% of the populations in riffles of cobble and pebbles densely covered by diatoms and filamentous algae; adult emergences occurred at water temperatures of 16–21°C, with adult male swarms 2–3 m aboveground where tree branches were used as lateral swarm markers (LeSage and Harrison 1980b). In an organically enriched small chalk stream in southern England this species occurred in low numbers only at an unpolluted station (Pinder and Farr 1987). The larval tubes of *C. trifascia* are constructed largely of detritus and filamentous algae or filamentous algae alone, and the stream in which stones occurred had a thin aufwuchs film except during summer, at which time large areas of stones had a *Cladophora* blanket (Brennan and McLachlan 1979). The species has been reported from periphyton in a large stream, the Danube, associated primarily with *Cladophora* (Janković 1973). It has been taken in low numbers from 2 of 5 stations receiving organic enrichment in the River Sar in Spain (Cobo and Gonzáles 1991). In Lebanon, *C. trifascia* occurred at 800–1200 m at several different stream sites, most of which had mosses or macrophytes; 1 station was polluted (Moubayed and Laville 1983). A population in a 3rd-order trout stream consisted of 2 cohorts that made up 9.7% of total secondary production of midges (Berg and Hellenthal 1992a, 1992b). The species, collected at a station with medium levels of zinc, was considered to be tolerant according to the pollution tolerance codes developed by Wilson and McGill (1982) (Armitage and Blackburn 1985). In New Mexico, *C. trifascia* was an uncommon species, occurring in the San Juan River, an upper tributary of the Colorado River, and in the upper Rio Grande (Sublette and Sublette 1979). Adults have been taken from the upper Arkansas River in Colorado at elevations ranging from 1431 to 2748 m elevation (Ruse et al. unpublished data).

DISTRIBUTION.—Saskatchewan to Ontario and New York, south to California, New Mexico, and North Carolina.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂P, 1 L, river mi 0.0, 947 m elev; 2 ♂♂, river mi 53.0, 847 m elev; 3 ♂♂, river mi 61.5, 826 m elev; 1 ♂P, river mi 74.3, 792 m elev; 1 ♂, river mi 98.0, 732 m elev; 1 Pex, river mi 151.2, 556 m elev. Other material: Specimens have been examined from throughout the range of this species, including extensive reared material from New Mexico.

Eudactylocladius dubitatus (Johannsen)

Orthocladius (Dactylocladius) dubitatus Johannsen 1942:72; type locality, NY.

Hydrobaenus dubitatus (Johannsen); Roback 1957:76, immature stages.

Orthocladius (Eudactylocladius) dubitatus Johannsen; Sublette 1967:507, review; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:31, in catalog.

Eudactylocladius dubitatus (Johannsen); Sublette and Sublette 1979:73, generic position, distribution.

DIAGNOSIS AND DISCUSSION.—The males of this genus can be separated from the closely related *Orthocladius* (s.s.) by the greatly reduced basidorsal and basiventral gonocoxite lobes. The pupa has distinctive paired spinulae patches on terga II or III–VI, lacks recurved hooks on tergum II, and has a short, smooth, saclike thoracic horn that arises from a short stalk. The male of *E. dubitatus* can be separated from other Holarctic species by its short anal point, basimedian gonocoxite lobes that are not produced, and an apically tapered gonostylus with a scarcely discernible dorsodistal carina (cf. Sublette 1967:505, Fig. 17). The pupa has been redescribed by Roback (1957:81: Figs. 194–196). Our material suggests that this species is more variable in the pupal stage than heretofore known: the weak, paired shagreen patches of tergum II may be reduced to just a few points, or even completely absent; the apical spinulae row on tergum VIII, in like manner, may be well developed, reduced to a few points, or even absent. A unique feature appears to be the presence of well-developed pedes spurii B on terga I, II, and III.

ECOLOGY.—*Eudactylocladius dubitatus* is probably madicolous since the pupae are sometimes taken in streams. The madicolous biotope occurs as a thin film of water on any solid substratum such as seeps on vertical rock faces, splash zones of rapids and waterfalls, water interface of emergent vegetation, and at stream margins. Spring runs provide a stable environment and will usually include members of this assemblage. The species, while rare in this system, has been collected on the upper Arkansas River of Colorado at elevations ranging from 1444 to 2143 m (Ruse et al. unpublished data). Species of this genus occur in lakes, temporary ponds, swamps, and in madicolous assemblages on rock faces and in moist soil (Cranston et al. 1989).

DISTRIBUTION.—California to New Mexico east to New York and Pennsylvania.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 Pex, river mi 124.6L, 625 m elev, 26-XI-91. Other material examined: reared specimens from California, Colorado, and New Mexico.

Eukiefferiella claripennis (Lundbeck)

Chironomus claripennis Lundbeck 1898:281; type locality, Greenland.

Eukiefferiella claripennis (Lundbeck); Oliver 1970: 102, lectotype; Lehmann 1972:359, adult, pupa, distribution, synonymy; Pinder 1974:198, Laville 1979:160, Wilson 1987:391 and 1989:373, ecology; Halvorsen 1981:34, review, female; Hudson et al. 1990:9, Oliver et al. 1990:26, catalog, distribution, synonymy; Langton 1991:125, pupa.

DIAGNOSIS AND DISCUSSION.—The adult male is characterized by having bare eyes, an absence of R_{2+3}, a moderately extended costa that ends slightly proximal to apex of M_{3+4} (Lehmann 1972: Fig.7), and, above all, the features of the male genitalia (Lehmann 1972: Fig. 6). The pupa has a distinctive thoracic horn and abdominal chaetotaxy (Lehmann 1972: Figs. 8, 9). The adult is very similar to *E. brevinervis* (Malloch) (Sublette 1970:71) but differs in having a lower antennal ratio (0.75–1.30; *E. brevinervis*, 2.0–2.4).

ECOLOGY.—*Eukiefferiella claripennis* is widely distributed in lower and medium elevation streams. It is eurythermous and rheobiontic (Lehmann 1972). Pinder (1980), Pinder and Farr (1987), and Pinder et al. (1987) collected it most often on *Ranunculus* and gravel substrates, while Ringe (1974), Halvorsen (1981), and Nolte (1991) reported it as an inhabitant of aquatic mosses. Halvorsen (1981) also found it on the surface of rocks in swiftly flowing water at 500 m elevation, and Millet et al. (1987) reported it from rocks with *Cladophora. E. claripennis* tolerates low to medium levels of zinc and is considered to be relatively tolerant according to the pollution codes of Wilson and McGill (1982) (Armitage and Blackburn 1985). Gower et al. (1994) reported this to be one of the most abundant and tolerant chironomids, occurring at stream stations with high levels of copper and aluminum. Pinder and Farr (1987) collected it from stations with elevated levels of organic enrichment in a small chalk stream in southern England, but not in numbers greater than at clean water stations. It has been taken from a calcareous stream with elevated levels of zinc but not from acid streams with higher levels of zinc (Wilson 1988), and is considered to be a moderately pollution-tolerant species (Bazerque et al. 1989). In Lebanon, Moubayed and Laville (1983) reported this species from a seasonal limnocrene in eddies at the outflow, with water temperatures ranging from 14° to 16°C; elevation was 850 m. Oliver and Sinclair (1989) regarded it as a member of the madicolous assemblage. According to Bode (1983), the *claripennis*-group is the most tolerant member of the genus, occurring from high-altitude streams to larger, warmer rivers. In the brown-water stream system studied by Boerger (1981) in Alberta, *E. claripennis* constituted only 0.5% of the Orthocladiinae males/m^2/yr. It is one of the predominant chironomids that emerged in the spring from the River Pang in England (Ruse 1992). Ringe (1974) observed 4 adult emergence periods from a small stream in central Germany, with most individuals emerging during the interval from June to August. In Austria, Schmid (1993) found low larval densities of this midge from a coldwater, gravel-bottomed stream. In Germany it has been reported from the Danube, a large river (Anderwald et al. 1991), as well as a regulated, primary tributary, the lower Inn River (Reiss and Kohmann 1982); in the Alz River this species avoids the soft sediments immediately below a lake outflow but is common farther downstream (Kownacki and Margreiter-Kownacka 1993). In the French Pyrenees the streams of the Ossau Valley support moderate numbers of *E. claripennis* at elevations from 500 to 800 m, in slow- to fast-moving water; maximum temperatures range from 15° to 18°C (Laville and Vinçon 1991). Ruse et al. (unpublished data) collected adults of this species at elevations ranging from 1431 to 2969 m in the upper Arkansas River in Colorado, from areas where substrata range from boulder-cobble to gravel-sand. In New Mexico *E. claripennis* occurs in all northern and western drainages in cool to cold waters where substrata are predominantly gravel-sand (Sublette and Sublette 1979).

Steep rock faces at or near the water's edge in Grand Canyon, together with the occasional patches of cobble-gravel, provide considerable madicolous habitat and are the probable preferred habitat.

DISTRIBUTION.—Holarctic; widely distributed in the Nearctic region; introduced into Hawaii (Oliver et al. 1990).

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂♂, river mi 0.0, 947 m elev; 1 ♀ Pex, river mi 3.4, 945 m elev; 4 ♂♂, river mi 31.5, 876 m elev; 1 ♂, river mi 31.8, 876 m elev; 1 ♀ Pex, river mi 34.1, 872 m elev; 1 ♂, river mi 43.2, 861 m elev; 1 ♂, river mi 61.5, 826 m elev; 2 ♂♂, river mi 65.3, 808 m elev; 1 ♂, river mi 98.0, 706 m elev; 2 ♂♂, river mi 108.5, 664 m elev; 3 ♂♂, river mi 133.0, 597 m elev; 1 ♂, river mi 150.0, 556 m elev; 1 ♂, river mi 172.0, 521 m elev; 1 ♂, river mi 204.0, 454 m elev; 1 ♂, 1 ♀ Pex, river mi 205.7, 451 m elev.

Eukiefferiella coerulescens (Kieffer)

Trichocladius coerulescens Kieffer, in Zavřel 1926:279.

Spaniotoma (Eukiefferiella) coerulescens (Kieffer); Edwards 1929:354, generic (subgeneric) position, review, distribution.

Eukiefferiella coerulescens (Kieffer); Brundin 1956:87, male, in key, generic position, distribution; Lehmann 1972:369, male, pupa; Hudson et al. 1990:9, in list, distribution; Langton 1991:124, pupa.

DIAGNOSIS.—In the adult the presence of distinct microtrichia between the eye facets and a bare squama are unique features among Nearctic *Eukiefferiella.* The pupa has a distinctive chaetotaxy as well as very short anal macrosetae, of which 1 is distinctly shorter than the other 2 (cf. Langton 1991: Figs. 51a–c).

DISCUSSION.—Nearctic material of adults and pupae agrees well with the descriptions given by Lehmann (1972:369) except that the antennal ratio of the male is intermediate between that given for this species and *E. boevrensis* Brundin. Langton (1991:124) has redescribed the pupa (in a correction sheet he has added that the pupa has a small, thin-walled, saclike thoracic horn; this is very frequently lost and thus in earlier descriptions was described as lacking). Our material agrees well with his description.

ECOLOGY.—Listed as a member of the madicolous assemblage by Oliver and Sinclair (1989) (see *Eudactylocladius dubitatus*, above), *E. coerulescens* has also been taken from aquatic mosses (Ringe 1974, Laville and Lavandier 1977, Nolte 1991) and has been found in streams with organic enrichment (Cobo and Gonzáles 1991). Bode (1983) reported the *coerulescens*-group as apparently widespread in North America, occurring mostly in small to medium-sized, unpolluted streams. Schmid (1993) collected it in low numbers from the surface and gravel interstices of a coldwater, gravel-bottomed stream in Austria. In Germany, Ringe (1974) observed that adult emergence in 2 small streams was essentially bivoltine but that the peaks of emergence were out of phase between the 2 streams, with the warmer stream having the main peaks of emergence almost a month before the stream with the colder, more uniform temperatures. In the Fulda, Lehmann (1971) found this species only in strongly flowing water in moss or on stones of the krenal to hyporithral regions. Kownacki (1982) found this species at only a single station in a small upland stream in Poland, occurring in an area of low current. Mouyabed and Laville (1983) reported this species in Lebanon from 3 stream systems at elevations above 1100 m, usually on moss- or algal-covered rubble. In the Ossau Valley of the French Pyrenees, *E. coerulescens* is one of the more abundant species, occurring most often in fast to very fast streams from 500 to 2100 m elevation; maximum temperatures range from 10° to 15°C (Laville and Vinçon 1991). One of the most unusual occurrences of *E. coerulescens* was reported in an underground stream of a cave system in Rumania some 8000 m from its epigyean source (Albu and Stergar 1971). Adults have been taken in the Arkansas River of Colorado at elevations ranging from 1431 to 1618 m, primarily from gravel-sand substrata (Ruse et al. unpublished data). In New Mexico *E. coerulescens* is found mostly in the cool to cold northern and western streams where gravel-sand substrata predominate; a record from the warm-water, lower Pecos River was from a gravel substratum (Sublette unpublished data).

DISTRIBUTION.—Holarctic; this species is probably more widely distributed in the Nearctic region than records indicate.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♀ P, river mi 0.0, 947 m elev; 1 ♂, river mi 3.4, 941 m elev; 1 ♂, river mi 31.5, 876 m elev; 2 ♂♂, river mi 43.2, 861 m elev; 1 ♂, river mi 68.0, 808 m elev. In addition, we have reared material from Arizona, Colorado, and New Mexico.

Eukiefferiella ilkleyensis (Edwards)

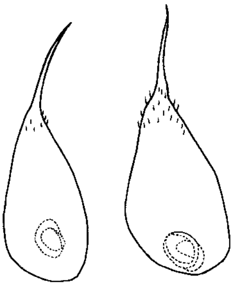
(Figs. 36–39)

Spaniotoma ilkleyensis Edwards 1929:349; type locality, Ilkley, Yorkshire, England.

Eukiefferiella ilkleyensis (Edwards); Lehmann 1972:372, revision, adult, pupa; Pinder 1974:198 and Laville 1979: 161, ecology; Storey 1987:339, developmental ecology; Hudson et al. 1990:9, in list, distribution.

Nearctic males and pupae, which are considered here as conspecific with Palearctic populations, differ in some slight details. The following descriptions define the Nearctic material.

MALE.—*Coloration*: Almost entirely blackish brown; scutellum, humeral and pleural areas yellowish; legs dark; abdomen blackish brown with the narrow apices of T VII and VIII somewhat paler; genitalia dark. Antenna with 13 flagellomeres. Antennal ratio 0.85–1.05 (10). Palpal proportions 62:101:101:164 µm. Eyes reniform, without dorsal extensions; ocular ratio 0.68–0.73 (4). Clypeus rectangular, much wider than long, slightly narrower at



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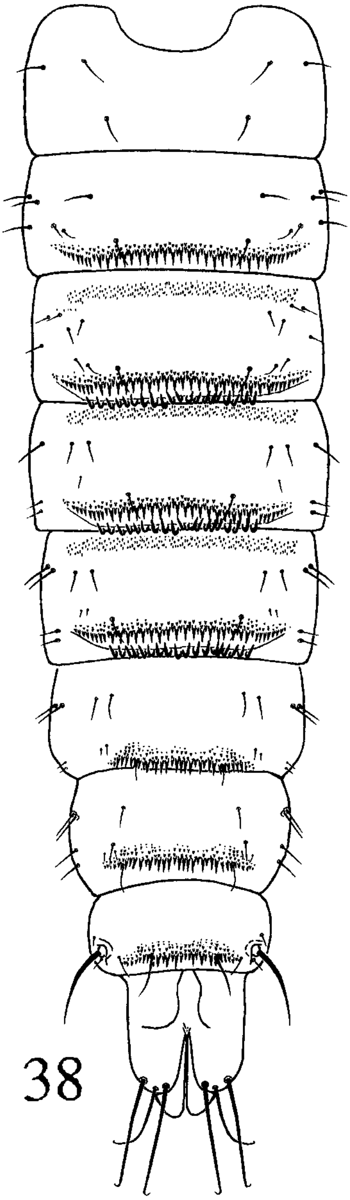

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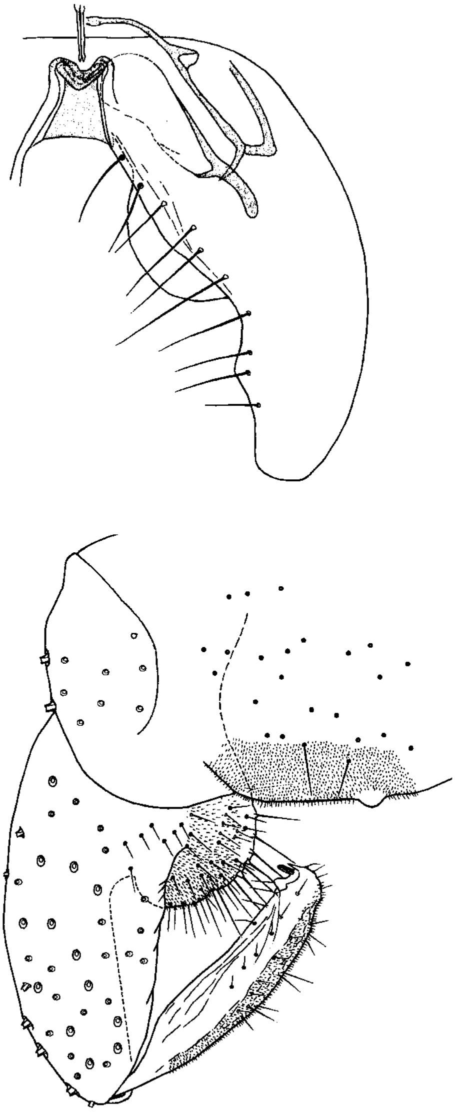


39

Figs. 37–39. *Eukiefferiella ilkleyensis.* Pupa: 37, thoracic horn; 38, abdominal shagreen and chaetotaxy. *Metriocnemus stevensi.* Male: 39, genitalia (dorsal view below, internal skeleton above).

base than width of the antennal pedicel; clyp/ped ratio 0.87–0.93 (9); clypeus with 6–8 (12) setae. Temporal setae 2–5 (12), usually in a small clump behind dorsal apex of the eye (with 1–2 very fine inner verticals observed in 2 specimens).

Thorax: Antepronotum slightly and almost evenly tapered to the apex, collarlike. Thoracic chaetotaxy: lateral antepronotals 2–5 (5); dorsocentrals 8–12 (5), set in paler alveoli, in a single row; acrostichials 7–13 (5), mostly in 2 rows; prealars 3 (5); supra-alars lacking; scutellars 7–11 (5), mostly in a staggered single row.

Wing: Membrane with very fine microtrichia barely visible at phase 500X. Costa extended 30–55 (6) µm beyond R_{4+5}, which ends distinctly proximal to tip of M_{3+4}. R_{2+3} ends at 0.29–0.35 (5) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.09–1.17 (5). Wing length 1.90–2.37 (9) mm. Squama with 6–13 (11) marginal setae. Wing vein setae: R 1–4 (5), R_1 0–1 (5), other veins without setae.

Legs: All legs with a single tibial spur; foretibial spur length 48–58 (5) µm; middle tibial spur length 38–46 (5) µm; hind tibial spur length 54–70 (5) µm. Pulvilli absent. Leg ratios: P I 0.60–0.66 (10); P II 0.48–0.55 (5); P III 0.57–0.61 (5). P III comb setae 12–14 (5). P II and P III sensilla chaetica lacking.

Abdomen: Setae on terga II–IV broadly strewn over most of each tergum except for a posteromedian concave area devoid of setae; terga V–VIII with setae strewn over most of each tergum except for a narrow apical transverse band.

Genitalia (Fig. 36): Ninth tergum with 2–3 (10) setae. Virga absent. Gc/Gs ratio 1.80–2.06 (5).

PUPA.—*Exuviae*: Exuviae almost entirely brown.

Cephalothorax: Frontal setae absent. Thoracic horn (Fig. 37), length 122–152 µm; apical denticles on the basal enlargement very weak or perhaps absent in some specimens. Cephalothorax almost smooth on either side of median suture. Precorneal setae with 1 long and 2 smaller setae. Dorsocentrals small, almost in a line, $Dc_{1,3}$ larger, $Dc_{2,4}$ smaller. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen length 1.59–1.90 mm. Shagreen pattern and chaetotaxy (Fig. 38). Pedes spurii B lacking. Terga II–VIII with posterior spines; T III–V with a continuous row of recurved hooks behind the spine row; hook number: III 17–24, IV 18–24, V 12–18. Sterna VI and VII with inconspicuous apical denticles. Tergum VIII with $L_{1,2,4}$ very fine; L_3 larger and heavier but not spinose. Anal macrosetae of unequal length, with the medial 1 smaller than the lateral 2; lateral macrosetal length 124–150 µm.

DIAGNOSIS AND DISCUSSION.—Despite some minor differences, this population is considered to be conspecific with the Palearctic *E. ilkleyensis* (Edwards) and is very similar to the Holarctic *E. devonica* (Edwards) in adult and pupal stages. The adult differs in having the ventral junction of the gonocoxites irregularly papillose and the apex of the phallopodeme weakly digitate (not always clearly visible, being dependent upon the orientation of the genitalia on the slide), while both Palearctic *E. ilkleyensis* and *E. devonica* have a smoothly rounded medial junction and the phallopodeme is not illustrated as digitate (cf. Lehmann 1972: Figs. 30, 34). Further, the temporal setae of this population are usually restricted to behind the dorsal apex of the eye while Palearctic *E. ilkleyensis* has a group of 3–4 setae near the midline in addition to the group behind the dorsal apex of the eye (cf. Lehmann 1972: Fig. 36). The antennal ratio is much higher than in *E. devonica.*

The pupa of this species can best be distinguished by the different thoracic horn. In Palearctic *E. ilkleyensis* the filament is short (cf. Lehmann 1972: Fig. 37) to very short (cf. Langton 1991: Fig. 51d), while in this population the filament is distinctly longer; further, the fine denticles at the base of the filament are usually distinct in *E. ilkleyensis,* whereas in this population the denticles are very sparse (visible only at phase 500X) or entirely absent. Although the thoracic horn is nearer to that illustrated for *E. devonica* (Lehmann 1972: Fig. 32), the filament, which is shorter than in that species, and the absence of apical hooks on sternum VIII clearly distinguish this species from *E. devonica.*

ECOLOGY.—*Eukiefferiella ilkleyensis* is a member of the *devonica*-group, which is associated with mosses and algae in small to large rivers (Bode 1983). It has been found most often on *Ranunculus* (Pinder 1980), *Ranunculus* and gravel (Pinder et al. 1987), or aquatic mosses (Ringe 1974, Nolte 1991). Armitage and Blackburn (1985) reported the species at stream sites with low zinc concentrations and considered it to be intolerant in the pollution tolerance codes of Wilson and McGill (1982). However, Cobo and Gonzáles (1991) collected it on the Sar River in Spain at 1 station of 5 that received organic enrichment. Pinder and Farr (1987) also reported it in low numbers from a small chalk stream in southern England at a station with elevated levels of organic enrichment. In Poland in the River San, Kownacki (1989) found this species to be one of the dominants above a sewage outfall, but it diminished or disappeared at downstream stations. Storey (1987) considered *E. ilkleyensis* to be a scraper/herbivore that selectively feeds on aufwuchs, especially epiphytic diatoms. Tokeshi and Townsend (1987) described aspects of the ecology of a population living epiphytically on *Myriophyllum spicatum* L. in a small river in eastern England. It was collected by Schmid (1993) from a coldwater, gravel-bottomed stream in Austria; larval densities were low. Kownacki and Kownacka (1971) and Kownacki (1982) found this species at several stations on small upland streams in Poland; however, greatest numbers were reported over stony bottoms. Kownacki and Zosidze (1980) and Kownacki (1985) also reported it from medium to large, stony streams from the Little Caucasus Mountains of Georgia (Adzhar) and the Caucasus Mountains of Azerbaijan. In the Alz River of Germany, Kownacki and Margreiter-Kownacka (1993) reported that this species avoids slower currents and softer bottoms below a lake outflow but occurs commonly in lower stretches of the stream. In Lebanon, Moubayed and Laville (1983) reported *E. ilkleyensis* at only 1 station on the Assi River, in fast current, on rubble partially covered with mosses. In the Ossau Valley of the French Pyrenees, this is a rare species occurring in fast to slow streams at elevations of 450–500 m; maximum temperature is 15°C (Laville and Vinçon 1991). Ruse et al. (unpublished data) found it at only a single location in the upper Arkansas River of Colorado at an elevation of 1431 m.

Distribution.—We have reared material from streams in Arizona, Colorado, and New Mexico.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂♂, 5 ♂P, 5 ♀ Pex, river mi 3.4, 941 m elev; 1 ♂ Pex, 1 ♀ Pex, river mi 34.1, 872 m elev; 1 Pex, river mi 63.7, 818 m elev; 1 ♂P, river mi 74.3, 792 m elev; 1 ♂, river mi 75.3, 785 m elev; 1 ♂, river mi 0.0, 947 m elev; 1 ♂, river mi 52.7, 846 m elev; 2 ♂♂, river mi 71.0, 808 m elev; 2 ♂♂, river mi 72.0, 796 m elev; 1 ♂, river mi 87.5, 740 m elev; 1 ♂, river mi 88.0, 739 m elev; 1 ♂, river mi 89.0, 736 m elev (CAS, USNM, CNC, INHS, JES).

Eukiefferiella sp.

Diagnosis, discussion, and ecology.—The adult is scarcely distinguishable from that of *E. ilkleyensis* in genitalic features; however, the tip of the antenna is broken off (antennal ratio estimated to be about 1.0). The pupa is readily distinguishable by its distinctive thoracic horn, which is more like that of *E. devonica* (Edwards) (Lehmann 1972: Fig. 32). Unfortunately, the presence of small hooks at the apex of S VII (Lehmann 1972: Fig. 33) cannot be ascertained, as the apex of the associated pupal exuviae is missing beyond segment V.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂ Pex, river mi 63.7, 818 m elev.

Limnophyes sp.

Diagnosis and discussion.—A single male was taken, but during slide preparation the genitalia were badly crushed, hence the lack of a specific determination.

Ecology.—The genus *Limnophyes* occurs in numerous ecotopes, ranging from aquatic (particularly madicolous) to semiterrestrial habitats.

Material examined.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 133.5, 600 m elev, 9-II-90.

Metriocnemus stevensi
Sublette, new species

Holotype male.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, Vaseys Paradise, river mi 31.8, 876 m elev, J.S. (CAS).

Coloration: Head, thoracic vittae, preepisternum, and postnotum blackish brown; antepronotum and scutellum paler than postnotum; humeral and pleural areas yellowish; legs and abdomen dark brown.

Head: Antenna with 13 flagellomeres; fully plumed. Antennal ratio 0.93. Palpal proportions 47:195:172:211 µm. Eyes with dorsal extension short and wedge-shaped. Ocular ratio

0.45. Clypeus quadrangular, slightly wider at base than width of the antennal pedicel (1.07); with 22 (23; 1) setae. Temporal setae 23 (31; 1), those in the postocular series coarse and in a single row, while those lying medial to the eye finer, multiserial, and reaching to near midline of the head.

Thorax: Antepronotum rather broad and collarlike, almost parallel-sided in the apical half. Thoracic chaetotaxy: lateral antepronotals 7 (9; 1); dorsocentrals 53 (42; 1) (including 15 [16; 1] humerals), in 3 staggered rows posteriorly, with the humerals becoming multiserial anteriorly; acrostichials about 35 (37; 1), partially in 2 rows; prealars 18 (23; 1); supra-alars 2 (2; 1); scutellars 32 (32; 1), in a single row laterally, becoming 3–4 rows medially; preepisternals 9 (5; 1).

Wing: Membrane with fine macrotrichia over most of the membrane. Costa extended 170 (126; 1) µm beyond R_{4+5}, which ends slightly distal to M_{3+4} at 0.21 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} almost parallel to R_1, ending at 0.14 of the distance between its apex and apex of R_{4+5}. Venarum ratio 1.24 (1.23; 1). Wing length 2.25 (1.92; 1) mm. Squama with 17 (19; 1) marginal setae. Wing vein setae: R 75, r-m 7, R_1 67, R_{4+5} 128, M 24, M_{1+2} 104, M_{3+4} 24, Cu 32, Cu_1 18, remigium 6.

Legs: Foretibial spur of holotype broken at tip (54; 1) µm; middle tibial spur lengths 31/31 (34/28; 1) µm (tip of longer spur on holotype broken); hind tibial spur lengths 53/28 (72/34; 1) µm (extreme tip of longer spur on holotype broken). Pulvilli vestigial. Tarsal pseudospurs present on Ta_{1-3} of P II and P III (P III tarsi missing on holotype). Leg ratios: P I 0.63; P II 0.43 (0.40; 1); P III (0.44; 1) (P III lacking on holotype). P III comb setae 11 (12; 1). P II and P III sensilla chaetica lacking (P III tarsi missing on holotype).

Abdomen: Abdominal terga with scattered setae; T IV with about 93 setae; sterna III–VI with a midventral row of setae, that of S III uniserial, S IV 2X with S V–VI multiserial; S II–VI with multiserial laterals; S VII–VIII with medial and lateral setal bands fused.

Genitalia (Fig. 39): Ninth tergum with 24 (21; 1) setae. Small virga present; length 24 µm. Gc/Gs ratio 1.78.

DIAGNOSIS AND DISCUSSION.—The combination of heavily haired wings, presence of preepisternal setae, and extremely short anal point is unique among Nearctic *Metriocnemus*.

ECOLOGY.—The genus *Metriocnemus* occurs in a wide variety of habitats, from madicolous to semiterrestrial habitats.

MATERIAL EXAMINED.—Paratype (and holotype) ♂, AZ: Coconino Co., Grand Canyon National Park, Colorado River, mi 31.8, 876 m elev, LES (CAS).

This species is dedicated to Dr. Lawrence E. Stevens who initiated and coordinated this study.

Orthocladius (Euorthocladius) luteipes Goetghebuer

Orthocladius luteipes Goetghebuer 1938:457; type locality, Austria.

Orthocladius (Euorthocladius) luteipes Goetghebuer; Soponis 1990:23, revision, adults and immatures, distribution.

DIAGNOSIS AND DISCUSSION.—The adult male and immatures have been separated in key by Soponis (1990). Males are similar to those of *Orthocladius (Euorthocladius) rivicola* Kieffer but may be recognized by the more square-shaped basidorsal gonocoxite lobe below which the basiventral gonocoxite lobe is more weakly projecting than in *O. rivicola*; however, the pupae are more distinctive than the adults. It is probable that some males identified in the literature as *O. rivicola* are actually *O. luteipes*.

DISTRIBUTION.—Palearctic; Oregon to New York, south to Arizona and Georgia.

ECOLOGY.—*Orthocladius luteipes* occurs in creek and riverine habitats, spinning gelatinous cases on stones. This species' distribution broadly overlaps that of *O. rivicola*.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 3.4, 941 m elev, 24-VII-71.

Orthocladius (Euorthocladius) rivicola Kieffer

Orthocladius rivicola Kieffer 1911:181; type locality, Germany.

Orthocladius (Euorthocladius) rivicola Kieffer; Laville 1979:161, ecology; Soponis 1990:26, revision, all stages, distribution; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:31, catalog, distribution.

DIAGNOSIS AND DISCUSSION.—Soponis (1990) has differentiated the adult and pupa of this species from other Holarctic members of the subgenus.

ECOLOGY.—*Orthocladius rivicola* has been categorized as "less pollution resistant" (Bazerque et al. 1989), although Cobo and Gonzáles

(1991) reported it at 3 of 5 stations receiving organic enrichment on the River Sar in Spain. In the high arctic Hayes and Murray (1987) found this to be one of the numerically dominant forms that exhibited a bimodal emergence during a 24-h study, with emergence continuing over the entire 6-wk study period. Laville and Lavandier (1977) also reported this as a numerically dominant species all along the length of a torrential brook in the Vallon d'Estaragne in the French Pyrenees. In the Ossau Valley of the French Pyrenees this was one of the "frequent or abundant" species in fast to very fast waters at elevations of 500–1500 m; maximum water temperatures were 12–15°C (Laville and Vinçon 1991). It has been reported from aquatic mosses (Kownacki 1971, Nolte 1991) and from *Cladophora* in the aufwuchs assemblage (Janković 1973). Mason and Lehmkuhl (1983) observed that numbers of this species were not diminished downstream from a dam when compared with upstream populations. In Austria, Schmid (1993) collected larvae in low numbers from the surface and gravel interstices in a coldwater stream, while Anderwald et al. (1991) took it from the Danube, a large river. It has also been reported from the lower Danube in the former Yugoslavia (Janković 1973). Ringe (1974) illustrated an emergence period from April to August in a small stream in central Germany, with 1 major peak of emergence occurring in early May; in the Fulda, Lehmann (1971) reported the highest abundance of this species in the strongly flowing currents of the rhithral regions. Kownacki (1982) found it to be most abundant in Poland at a station on stony bottoms in an upper-elevation Carpathian pastureland stream, while in the high Tatras it was most often encountered in rapid current in the montane forest zone (700–1500 m elevation), being the dominant species there (Kownacki 1971, Kownacki and Kownacka 1971). Kownacka and Kownacki (1972) clarified the dominant status to those stations with a granite substratum below 1550 m elevation. In the medium to large stony streams of the Little Caucasus Mountains of Georgia (Adzhar) and the Caucasus Mountains of Azerbaijan, this species was among the dominant chironomids (Kowanacki and Zosidze 1980, Kownacki 1985). In Rybi Potok, a polluted stream in Poland, Kownacki (1989) found that *O. rivicola* increased in abundance as organic enrichment decreased. In Germany, Kownacki and Margreiter-Kownacka (1993) collected it in the Alz River at all stations including the soft-bottomed, slower-flowing section immediately below a lake outflow; Reiss and Kohmann (1982) collected it from the banks of the lower Inn River, a large, regulated, primary tributary of the Danube. Fahy (1975) found highest numbers in low to intermediate flows in a low-nutrient, stony stream in Ireland. This is one of the more abundant orthoclads in the Colorado River as well as the upper Arkansas River in Colorado (Herrmann et al. unpublished), and the upper Canadian, Rio Grande, San Juan, and Gila drainages in New Mexico; it occurs on a variety of substrata ranging from boulder-gravel to sand-silt (Sublette unpublished). Ruse et al. (unpublished data) collected adults in the upper Arkansas River at elevations ranging from 1431 to 3042 m.

DISTRIBUTION.—Holarctic; widely distributed throughout much of North America from the high arctic to the lower temperate zones.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂♂, 2 ♀P, 1 Pex, river mi 0.0, 947 m elev; 1 ♂, river mi 2.0, 945 m elev; 3 ♂ Pex, river mi 3.4, 941 m elev; 1 ♂, river mi 20.4, 911 m elev; 1 ♂, river mi 31.0, 876 m elev; river mi 31.5, 876 m elev; 1 ♂, river mi 43.2, 861 m elev; 2 ♂♂, river mi 52.7, 846 m elev; 2 ♂♂, river mi 53.0, 846 m elev; 1 ♂, river mi 56.0, 838 m elev; 2 ♂♂, river mi 61.0, 826 m elev; 2 ♂♂, river mi 63.7, 823 m elev; 2 ♂♂, river mi 65.3, 815 m elev; 1 ♂, river mi 88.0, 739 m elev; 1 ♂, river mi 89.0, 736 m elev; 2 ♂♂, river mi 108.0, 699 m elev; 1 ♂, river mi 124.0, 625 m elev.

Orthocladius (Orthocladius) frigidus (Zetterstedt)

Chironomus frigidus Zetterstedt 1838:812; type locality, Greenland.

Orthocladius (Orthocladius) frigidus (Zetterstedt); Soponis 1987:123, subgeneric position, review, synonymy; 1990:53, morphology; Oliver et al. 1990:32, in catalog.

DIAGNOSIS AND DISCUSSION.—Soponis (1987) has characterized all life history stages. The male genitalia are similar to those of some members of the subgenus *Euorthocladius* (Soponis 1990) in which *O. frigidus* was, until recently, included. However, the anal point is usually distinctly broader and the dorsal extension of the eye is longer than in members of that subgenus (Soponis 1990: Fig. 12).

ECOLOGY.—*Orthocladius frigidus* inhabits cool to cold streams, constructing detritus-encrusted silken tubes in moss or algae. It has been reported on stones but seldom on moss and algae in a small stream in central Germany (Ringe 1974), on aquatic mosses (Nolte 1991), from "springs, streams and rivers" (Aagaard et al. 1987), and in an islandic lake, primarily in the littoral splash zone but occasionally as deep as 30 m (Lindegaard 1980). Armitage and Blackburn (1985) found *O. frigidus* in streams with moderate levels of zinc, but it is considered pollution intolerant in the classification of Wilson and McGill (1982). Serra-Tosio (1977) took it from a stream with considerable anthropogenic enrichment, while Cobo and Gonzáles (1991) reported it from 1 of 5 stations receiving organic enrichment on the River Sar in Spain. In a Pyrenean torrent, d'Estaragne, Laville and Lavandier (1977) found this species in small numbers above 2150 m elevation, occurring on boulder-gravel substrata or on moss. In the Ossau Valley in the French Pyrenees, this species had the highest frequency of occurrence, occupying streams at elevations of 500–2000 m; water temperatures ranged from 9° to 16°C (Laville and Vinçon 1991). Schmid (1992) observed this species at significantly higher densities in the main current channel than in the marginal area of a gravel stream, the Oberer Seebach, in Austria; he further reported a tendency towards bivoltinism. Ringe (1974) illustrated 2 major peaks of adult emergence from a small stream in central Germany, 1 in May and the other in November. Fahy (1975) collected this species most often in intermediate flows in a stony, low-nutrient stream system in Ireland. In the high Tatras of Poland it occupied stony bottoms in rapid current (Kownacki 1971, Kownacki and Kownacka 1971); in the Little Caucasus Mountains of Georgia (Adzhar) and in the high Caucasus Mountains of Azerbaijan it was taken from several stations in medium to large, stony-bottomed streams (Kownacki and Zosidze 1980, Kownacki 1985). In Germany, Kownacki and Margreiter-Kownacka (1993) found this species in the Alz River most often some distance below a lake outflow; Lehmann (1971) reported it from the Fulda in areas with strong currents; and Reiss and Kohmann (1982) collected it from the banks of the lower Inn River, a regulated, primary tributary of the Danube. In Lebanon, Moubayed and Laville (1983) reported *O. frigidus* from several stream systems with variable current and substrata, but usually at stations with mosses or macrophytes. It has been taken at elevations from 1746 to 3042 m on gravel/cobble substrates in the Arkansas River of Colorado (Ruse et al. unpublished data). The rarity of *O. frigidus* in the Colorado River is possibly due to the almost constant scouring action of the river in the canyon, which disturbs the preferred gravel and removes algal clumps.

DISTRIBUTION.—Holarctic; in North America this species occurs from California to New Mexico and Colorado, Pennsylvania, and Greenland.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 L, river mi 0.0.

Orthocladius (Orthocladius) mallochi Kieffer

Orthocladius lacteipennis Malloch 1915:524, male; type locality, South Haven, MI.

Orthocladius mallochi Kieffer 1919:191, *nomen novum* for *Orthocladius lacteipennis* Malloch 1915, *non* Lundström 1910.

Orthocladius (Orthocladius) mallochi Kieffer; Soponis 1977:63, revision, adults, immatures, distribution; Savage and Soponis 1983:302, adult morphology; Hudson et al. 1990:11, in list, distribution; Oliver et al. 1990:32, in catalog, distribution.

DIAGNOSIS AND DISCUSSION.—Adults and immatures have been keyed by Soponis (1977).

ECOLOGY.—*Orthocladius mallochi* was one of the rarest Orthocladiinae in a brown-water stream in Alberta, with only 0.03 of 1.0% males/m^2/yr collected (Boerger 1981). It is common in the upper Arkansas River of Colorado where it occurs at elevations of 1431–2905 m (Ruse et al. unpublished data). It occurs in most stream systems in New Mexico (Sublette unpublished).

DISTRIBUTION.—This species has an unusual distribution, with specimens taken from Alberta south to California and New Mexico in western North America and from Northwest Territories south to Illinois and South Carolina in the East.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 204.0.

Paracladius conversus (Walker)

Chironomus conversus Walker 1856:175; type locality, British Isles.

Paracladius conversus (Walker); Hirvenoja 1973:94, revision, adults and immatures; Sublette and Sublette 1979:

80, distribution; Oliver et al. 1990:33, in catalog, distribution.

DIAGNOSIS.—The adults and pupae of the 3 known species have been separated in key by Hirvenoja (1973). Reared material from New Mexico agrees well with Hirvenoja's descriptions as does the single male taken in Grand Canyon.

ECOLOGY.—*Paracladius conversus* is most frequently collected from lakes but is also known from slow-moving streams (Hirvenoja 1973). In Germany, Reiss and Kohmann (1982) collected it from stream margins of the lower Inn River, a large, regulated, primary tributary of the Danube; in the Fulda, Lehmann (1971) reported it from the Potamal region ("Barbenregion"). In the Nida River in Poland, Kownacki (1989) found this species to be generally distributed but occurring in greater abundance in the recovery zone below a sewer outfall. It is known from a zinc-contaminated stream where it constituted <0.5% of the sample (Wilson 1988). It has been statistically associated with *Myriophyllum* in the River Pang in England (Ruse 1992). In the Ossau Valley of the French Pyrenees this was a rare species, occurring in medium to slow streams at 800–850 m elevation; maximum water temperatures were 16° to 18°C (Laville and Vinçon 1991). In small, interrupted stream systems of Lebanon this species was found at 3 stations with macrophytes (Moubayed and Laville 1983). In New Mexico it was often taken near stream margins (Sublette and Sublette unpublished data).

DISTRIBUTION.—Arizona to New Mexico and Colorado; Pennsylvania. It is possible that some records of *P. alpicola* (Zetterstedt) from the Nearctic region are actually this species.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂♂, river mi 246L, 365 m elev, 13-XI-1975.

Parakiefferiella subaterrima (Malloch)

(Figs. 40–43)

Camptocladius subaterrimus Malloch 1915:512, male; type locality, bank of Mississippi River, Grand Tower, IL (INHS).

Parakiefferiella torulata Sæther 1969:138, male with associated pupal and larval exuviae; type locality, Whiteshell Park, Manitoba, ditch.

Maricladius subaterrimus (Malloch); Sublette 1970:85, generic position, review.

Parakiefferiella subaterrima (Malloch); Cranston and Oliver 1988:443, generic position, review, synonymy, distribution.

Parakiefferiella subaterrima (Malloch); Oliver et al. 1990:33, in catalog, distribution.

DIAGNOSIS AND DISCUSSION.—The male can be recognized by the presence of a distinct R_{2+3} which becomes evanescent apically, an antennal ratio usually about 1.0 (0.68–1.34), and, above all, the male genitalia. The genitalia (Fig. 40) have typically a bluntly acute anal point; compression due to more or less flattening by the cover glass results in considerable variation in appearance of the anal point as well as the basidorsal and basiventral gonocoxite lobes. Proximally, the basidorsal gonocoxite lobe usually has visible a transverse apodeme that appears as a darkened bar. Northern specimens have a higher number of anal point setae and higher antennal ratio (based on Sæther 1969).

The pupa, based on extensive rearings from New Mexico, differs in some features from that described by Sæther (1969): the frontal apotome has small frontal setae (Fig. 41), there is a small egg-shaped thoracic horn with fine apical denticles present (Fig. 42), pedes spurii B are present on T II and III, and the shagreen pattern on the abdomen is much weaker (Fig. 43). Specimens from the Chama River in New Mexico near the Colorado state line have heavier shagreen than those taken from the Rio Grande in Doña Ana County in New Mexico near the Texas state line. Thus, the pupa described from Manitoba (Sæther 1969) with the terga almost completely covered by shagreen may represent the extreme of a north–south cline.

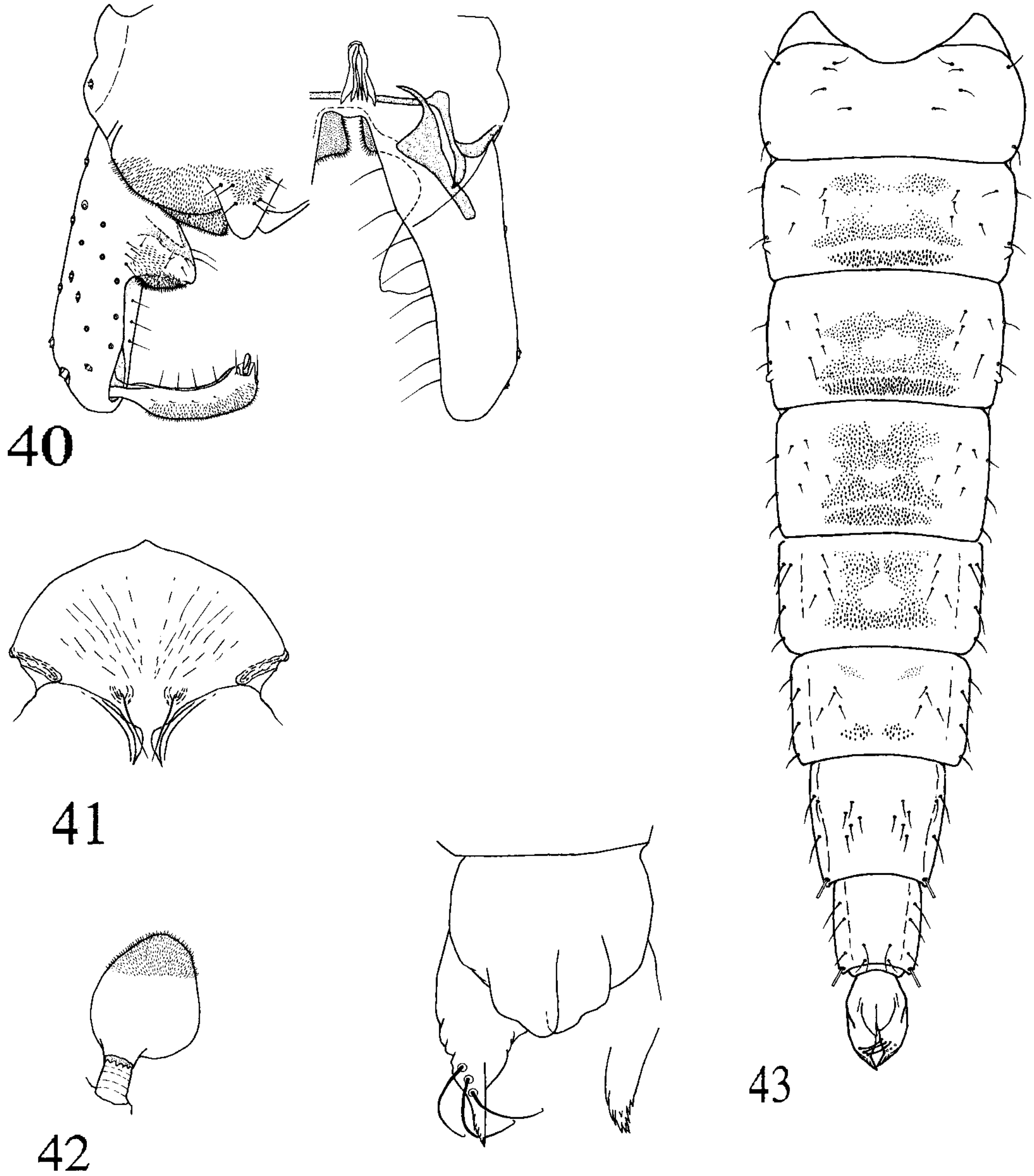
ECOLOGY.—This is a common inhabitant of the upper Arkansas River in Colorado, found at elevations ranging from 1444 to 2771 m (Ruse et al. unpublished data).

DISTRIBUTION.—Northwest Territory east to Quebec and south to California and Illinois.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 89.0, 732 m elev, 8-I-91. Other material examined: California, Colorado, New Mexico, and Utah.

Parametriocnemus lundbeckii (Johannsen)

Metriocnemus lundbeckii Johannsen 1905:302, *nomen novum* for *Chironomus nanus* Lundbeck 1898:285, *non* Meigen 1818; type locality, Greenland; Oliver et al. 1990: 34, in catalog, distribution; Epler 1995:6.65, larva, distribution.



Figs. 40–43. *Parakiefferiella subaterrima.* Male: 40, genitalia. Pupa: 41, frontal apotome; 42, thoracic horn; 43, abdominal chaetotaxy and shagreen, including details of anal lobe and apex of anal lobe.

Parametriocnemus lundbecki (Johannsen); Sublette 1967:537, review; Sæther 1969:115, review, synonymy, distribution; Simpson and Bode 1980:56, larva, ecology; Cranston et al. 1983:261, larva; Simpson 1983:320, ecology; Coffman et al. 1986:265, pupa; Cranston et al. 1989: 310, male; Hudson et al. 1990:11, in list, distribution.

DIAGNOSIS AND DISCUSSION.—The adults and pupae have been well characterized by Sæther (1969).

ECOLOGY.—The North Carolina biotic index (NCBI) value for *Parametriocnemus lundbeckii* is 3.7 (Lenat 1993), which agrees with the Simpson and Bode (1980) observation that the species is restricted to relatively clean water. It has been listed by Singh and Harrison (1984) as having 3 periods of adult emergence, but the species was not commonly taken, comprising only 1.84% of all chironomids collected; this was similar to Boerger's (1981) findings, which listed only 0.5 of 1.0% males/m^2/yr of the total Orthocladiinae. The cohort growth is asynchronous with maximal growth in the spring (Berg and Hellenthal 1992a). Beckett (1992) collected the species in a large temperate river on artificial plate samplers in low numbers during most months except June–August. *P. lundbeckii* was more frequently taken from an acid, poorly buffered Precambrian Shield stream with a boulder-cobble bottom covered with thick growths of *Fontinalis* (Rempel and Harrison 1987). McShaffrey and Olive (1985) found only diatoms in the gut contents of larvae. In the upper Arkansas River of Colorado this is an uncommon, but rather widely distributed, species occurring at elevations ranging from 1444 to 3042 m (Ruse et al. unpublished data). In New Mexico *P. lundbeckii* is widely distributed in northern and western cool- to coldwater streams (Sublette and Sublette 1979). Epler (1995) reported the larvae as being sensitive to organic pollution.

DISTRIBUTION.—Alberta east to Quebec and Greenland, south to California and Florida.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 133.5, 625 m elev, 17-VIII-75.

Paraphaenocladius exagitans (Johannsen)

Metriocnemus exagitans Johannsen 1905:303; type locality, New York.

Paraphaenocladius exagitans (Johannsen); Sublette 1967:543, review, generic position; Hudson et al. 1990:12, in list, distribution; Oliver et al. 1990:34, catalog, distribution, synonymy.

DIAGNOSIS AND DISCUSSION.—The hairy wings, retracted R_{4+5} ending proximal to the apex of M_{3+4}, and features of the male genitalia (Sublette 1967: Figs. 36, 37) differentiate this species from other Nearctic congeners.

ECOLOGY.—Members of this genus in the Palearctic region are reported to be terrestrial, living in damp soil adjacent to water bodies (Strenzke 1950). In the Nearctic, however, "at least semiaquatic and perhaps truly aquatic species occur in streams and springs" (Cranston et al. 1983). Rosenberg et al. (1988) reported *Paraphaenocladius exagitans* emerging from a fen in western Ontario, indicating at least a semiaquatic existence for this species. Ruse et al. (unpublished data) collected this species only once along the Arkansas River in Colorado at an elevation of 2338 m; adults probably came from nearby spring seeps or marshy areas.

DISTRIBUTION.—South Dakota east to New York, south to Arizona and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 31.8, 876 m elev; 1 ♂, river mi 124.0, 625 m elev.

Pseudosmittia nanseni (Kieffer)

Psectrocladius nanseni Kieffer 1926:82; type locality, Ellesmere Island, Northwest Territories.

Prosmittia nanseni (Kieffer); Oliver 1963:177, generic position, in list; Sæther et al. 1984:270, review of holotype.

Pseudosmittia nanseni (Kieffer); Cranston and Oliver 1988:451, generic position, added description of male, distribution; Hudson et al. 1990:13, in list, distribution.

Pseudosmittia n. sp.1; Sublette and Sublette 1979:83, misidentification, distribution.

DIAGNOSIS.—The male genitalia (Sæther et al. 1984: Fig. 12; Cranston and Oliver 1988: Fig. 20) are distinctive. Immature stages are unknown.

DISCUSSION.—This wide-ranging species shows considerable variation between northern and more southern populations (Cranston and Oliver 1988). Dr. O.A. Sæther, University of Bergen, suggests the nominal species is actually a complex of related forms (personal communication).

ECOLOGY.—*Pseudosmittia nanseni* is probably a madicolous species, as Wrubleski and Rosenberg (1990) reported low numbers of it from emergent vegetation where apparently the aquatic-terrestrial interface provides a habitat. Presumably, wet algal strands in the splash zone on the rock faces of the canyon wall in Grand Canyon are similar to the interface found on emergent aquatic vegetation.

DISTRIBUTION.—Alaska to Greenland, south to California, east to Georgia.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 6.0, 945 m elev.

Tvetenia vitracies (Sæther)

Eukiefferiella vitracies Sæther 1969:49, male, female, and pupa.

Tvetenia vitracies (Sæther); Sæther and Halvorsen 1981:271, generic position; Coffman et al. 1986:293, pupa.

Tvetenia calvescens (Edwards); Sublette and Sublette 1979:74, review, distribution, misidentification.

DIAGNOSIS AND DISCUSSION.—The genitalia are very similar to those of *Tvetenia calvescens* (Edwards), *T. discoloripes* (Goetghebuer), and *T. bavarica* (Goetghebuer) (cf. Pinder 1978: Figs. 105 b, c; Lehmann 1972: Figs. 65, 70, 71, 77); however, the antennal ratios of *T. calvescens* (Edwards) and *T. bavarica* (Goetghebuer) are much lower (0.6–0.8 vs. 1.03–1.35). The pupal thoracic horn and abdominal chaetotaxy of *T. vitracies* have been briefly described by Sæther (1969) and figured by Coffmann et al. (1986: Fig. 9.75). It is very similar to that of *T. verralli* (Edwards) (Langton 1991), but the pupa of that species lacks the fine-pointed spines at the apex of the anal lobe. The adult male of *T. verralli* has much stronger crista dorsalis on the gonostylus (cf. Pinder 1978: Fig. 105A).

ECOLOGY.—Larvae of the *discoloripes*-group are most frequently found in larger, warmer rivers, most often in association with *Cladophora* (Bode 1983). Ruse et al. (unpublished data) collected *T. vitracies* in the upper Arkansas River of Colorado at elevations ranging from 1497 to 1879 m.

DISTRIBUTION.—Arizona, California, Colorado, New Mexico, Ontario, and Saskatchewan. Possibly, some of the North American records of *T. calvescens* are actually this species since the male genitalia appear to be virtually indistinguishable.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 5 ♂♂, river mi 31.5, 876 m elev; 6 ♂♂, river mi 31.8, 876 m elev; 1 ♂, river mi 43.0, 861 m elev; 3 ♂♂, river mi 94.9, 715 m elev; 2 ♂♂, river mi 61.0, 826 m elev; 1 ♂, river mi 123.0, 632 m elev; 1 ♂, river mi 135.0, 594 m elev; 2 ♂♂, river mi 186.0, 491 m elev; 1 ♂, river mi 204.0, 454 m elev; 1 ♂, river mi 225.0, 411 m elev.

SUBFAMILY CHIRONOMINAE

Tribe Chironomini

Apedilum subcinctum Townes

Apedilum subcinctum Townes 1945:33; type locality, Reno, NV; Epler 1988:112, review, generic reassignment; 1995:7.24, larva, distribution; Hudson et al. 1990:26, in list, distribution.

Paralauterborniella subcincta (Townes); Pinder and Reiss 1986:418, pupa.

Paralauterborniella subcincta subcincta (Townes); Bath and Anderson 1969:172, larva.

DIAGNOSIS AND DISCUSSION.—The male is recognized most readily by the features of genitalia (cf. Townes 1945: Fig.24; Epler 1988: Fig. 1e–k). The pupa has been characterized by Pinder and Reiss (1986) and Epler (1988).

ECOLOGY.—*Apedilum subcinctum* lives in aquatic vegetation, including mat algae. It sometimes becomes a pest in concrete-lined irrigation canals.

DISTRIBUTION.—California to Ontario, south to Jalisco.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 61.0, 826 m elev; also, material from California, Colorado, New Mexico.

Chironomus decorus
Johannsen

Chironomus decorus Johannsen 1905:239; type locality, Ithaca, NY; adults and immature stages.

Chironomus decorus Johannsen; Sublette and Sublette 1979:86, review, distribution; Martin et al. 1979:131, karyotype.

DIAGNOSIS AND DISCUSSION.—The male genitalia (Townes 1945: Fig. 136a), together with abdominal coloration consisting of saddle-shaped darker markings on terga II–V (heaviest on II–IV, occasionally evanescent on V) and a foretarsus without a beard, will differentiate the species. However, there are at least 10 Nearctic species in this complex (Martin et al. 1979), and identifications are somewhat uncertain at this time. One of the authors (JES) has examined the holotype at Cornell University, and the Grand Canyon material cannot be separated from it on adult morphology. The larva and pupa cannot be adequately separated. The most reliable separation remains through karyological examination.

ECOLOGY.—*Chironomus decorus* is primarily lentic but occurs widely in stream systems in backwater pools and river stretches with little current. As do other members of the genus, this species lives on soft, muddy substrata, occasionally on sandy-silt. In New Mexico it occurs in every major stream system in the state (Sublette and Sublette 1979).

DISTRIBUTION.—Throughout much of North America; however, many of the literature records of this and its junior synonym, *Chironomus attenuatus* Walker, are suspect. Karyological or DNA studies are needed to define the many populations.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 259.0R, 8-V-90; 1 ♂, river mi 268.5, 21-VII-75, LES.

Chironomus (Chironomus) decorus Johannsen complex

At least 2 additional species of this group occur in Grand Canyon, based on males with adequate genitalia visible in limited slide-mounted material. However, this material was not considered sufficient upon which to base new species descriptions. With additional material in hand a better appraisal will be possible. The localities for these are described below

Chironomus n. sp. 1

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 ♂, river mi 246.0L, 13-XI-75; ? 1 ♀, Pex, river mi 209.0L, 4-XII-91.

Chironomus n. sp. 2

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 269.5, 21-VII-75.

Chironomus (Chironomus) utahensis Malloch

Chironomus utahensis Malloch 1915:438; type locality, Kaysville, UT; Schaller and English 1976:300, cytology; Sublette and Sublette 1979:89, distribution; Martin et al. 1979:139, karyotype.

Tendipes (Tendipes) utahensis (Malloch); Townes 1945: 127, review.

Chironomus (Chironomus) utahensis Malloch; Oliver et al. 1990:43, distribution; Wülker et al. 1991:71, review, immatures and adults, karyosystematic position.

DIAGNOSIS AND DISCUSSION.—The distinctive male genitalia will serve to differentiate this species from other Nearctic species (cf. Townes 1945: Fig. 143). Immatures have been characterized by Wülker et al. (1991).

ECOLOGY.—*Chironomus utahensis* is primarily lentic, inhabiting water bodies ranging from large lakes and reservoirs to shallow ponds in Manitoba and playa lakes on the Llano Estacado of New Mexico. This species is an uncommon inhabitant of pool environments with silty sand substrata; it also may occur in backwaters. Similar collections of the lentic *C. decorus* complex have been taken in the Arkansas River in Colorado and Pecos River and Rio Grande in New Mexico (Sublette unpublished data).

DISTRIBUTION.—This widely distributed western species ranges from Alberta and Manitoba south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, 1 ♂ Pex, 1 Lex, river mi 53.0, 847 m elev; ? 1 ♀, river mi 0.0R, 11-VII-90, J.S.; ? 1 ♂, L, Pex, river mi 31.0R, 1-II-90, J.S.

Cyphomella gibbera Sæther

Cyphomella gibbera Sæther 1977:103; type locality, Yankton, SD, male, pupa; Pinder and Reiss 1986:379, pupa; Oliver et al. 1990:45, distribution.

DIAGNOSIS AND DISCUSSION.—The male is very near *Cyphomella cornea* Sæther in genitalic features but differs in having 8–11 setae on the inferior volsella while *C. cornea* has 0–1; the superior volsella lacks setae while in *C. cornea* there are usually 4 (cf. Sæther 1977: Figs. 37D, F). Immature stages have been figured by Sæther (1977: pupa, Fig. 37A, B; larva, Fig. 38; Pinder and Reiss 1983: larva, Fig. 10.13) as *Cyphomella* sp.

ECOLOGY.—Ruse et al. (unpublished data) collected this species in the upper Arkansas River of Colorado at an elevation of 1497 m. In New Mexico this species occurs in a wide variety of habitats ranging from cold- to warm-water streams with substrata ranging from gravel to sand-silt (Sublette and Sublette 1979).

DISTRIBUTION.—Saskatchewan and South Dakota south to Arizona and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 2 LL, river mi 61.0, 826 m elev; 1 L, river mi 87.5, 740 m elev; 1 L, river mi 187.5, 488 m elev, 19-IX-91, M.S.

Phaenopsectra profusa (Townes)

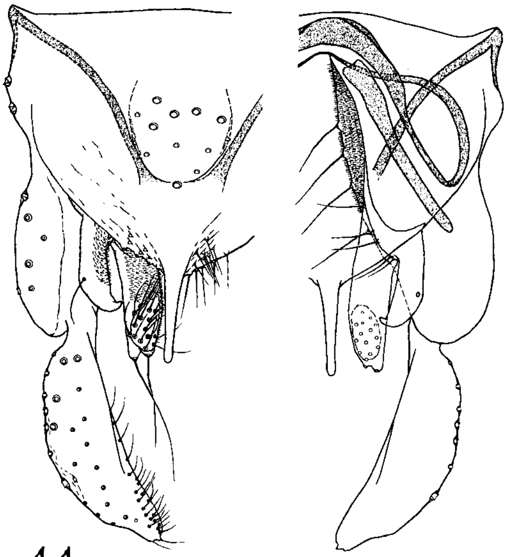
(Figs. 44–48)

Tanytarsus (Tanytarsus) profusus Townes 1945:73; type locality, Reno, NV, male.

Phaenopsectra profusa (Townes); Grodhaus 1987:137, generic position, morphology, ecology; Oliver et al. 1990:51, distribution.

Phaenopsectra n. sp. 1; Sublette and Sublette 1979:103, distribution, misidentification; Martin et al. 1979:151, karyotype.

The male has been briefly described by Townes (1945). The following is given to supplement his description.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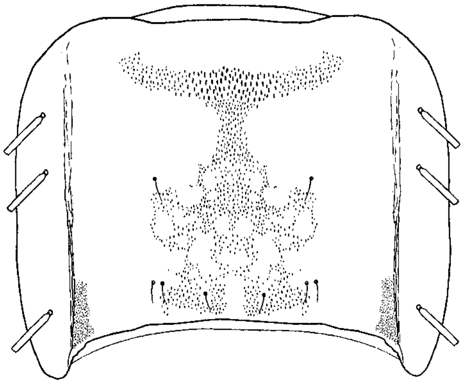
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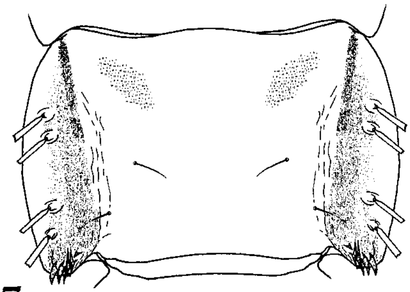
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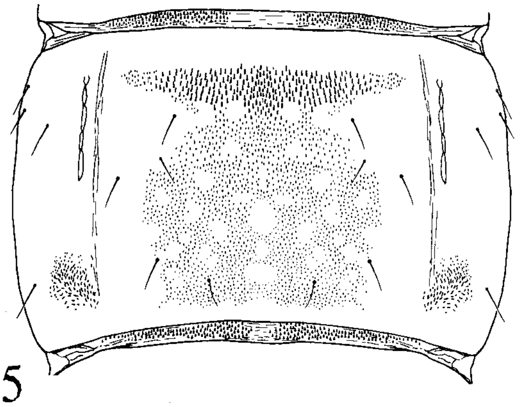
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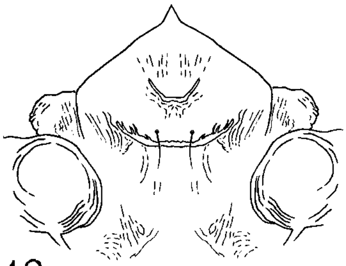
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Figs. 44–48. *Phaenopsectra profusa.* Male: 44, genitalia. Pupa: 45, tergum IV; 46, tergum VI; 47, tergum VIII. *Polypedilum (Polypedilum) obelos.* Pupa: 48, frontal apotome.

MALE.—*Coloration*: Head, thorax, and abdomen largely blackish brown; scutellum somewhat paler brown; legs with coxae dark, remainder mostly stramineous except knees, which are slightly darker; haltere knob pale; abdomen largely dark with the posterolateral margins of the terga paler brown; genitalia infuscate.

Head: Antenna with 13 flagellomeres. Antennal ratio 1.9–1.96. Palpal proportions 70:164: 179:289 μm. Eyes with dorsal extension long and parallel-sided. Ocular ratio 0.19. Clypeus quadrangular, slightly longer than wide, with 21–23 setae; clyp/ped ratio 0.76. Temporal setae 14, in a single row, reaching about halfway from the dorsal apex of the eyes to the midline of the head.

Thorax: Antepronotum greatly narrowed near the dorsal apex and closely appressed to the mesonotal continuation (cf. Townes 1945: Fig. 230). Thoracic chaetotaxy: lateral antepronotals lacking; dorsocentrals 16–18, in a partial double row; acrostichials 15–16, mostly in 2 rows; prealars 7; supra-alars lacking; scutellars 24–32, in a strewn pattern.

Wing: Membrane with heavy macrotrichia distal to the apex of R_1 and with sparse macrotrichia extending almost to the wing base. Costa not extended beyond R_{4+5}, which ends considerably distal to M_{3+4} at 0.93 of the distance between apex of M_{3+4} and M_{1+2}. R_{2+3} closely parallels R_1, ending at about 0.2 of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.0–1.04. Wing length 2.75–2.79 mm. Squama with 15–18 marginal setae. Wing vein setae: R 27, R_1 35, R_{4+5} 63, M_{1+2} 48, M_{3+4} 21, Cu_1 19, An 25.

Legs: Foretibial scale with a minute spine, very similar to that illustrated by Townes (1945: Fig. 249); middle tibial combs with a single spur; hind tibial combs with 2 spurs, of which 1 is slightly shorter than the other. Pulvilli conspicuous, almost as long as the claws. Leg ratios: P I 1.10–1.15; P II 0.57; P III 0.73.

Abdomen: Abdominal tergal setae scattered, becoming denser at the lateral margins.

Genitalia (Fig. 44): Ninth tergum with 12–16 setae. Gc/Gs ratio 0.95.

PUPA.—*Cephalothorax*: Cephalothorax brown; wing sheaths mostly pale but outlined with brownish margins. Frontal setae present on the frontal tubercles very similar to that illustrated for *P. flavipes* (Meigen) (cf.Pinder and Reiss 1986: Fig. 10.59A); frontal setal length 58 µm. Thoracic horn base also similar to that of *P. flavipes* (cf. Pinder and Reiss 1986: Fig. 10.59C). Median suture with strong tubercles on either side near the anterior end and with a smaller patch near the posterior end on either side. Precorneal setae very weak, with 1 longer and 2 slightly shorter setae. Posterior dorsocentrals small, in a line below the posterior tubercle patch; anterior dorsocentrals not discernible. Wing sheaths without bacatiform papillae or nasiform tubercles.

Abdomen: Abdomen mostly pale but with blackish spots at the corners of conjunctiva I–II, II–III, III–IV, and IV–V; lateral margins of terga V–VIII with a narrow brown band that becomes progressively broader posteriorly. Abdomen length 4.85–5.00 mm. Shagreen pattern and chaetotaxy very similar to *P. flavipes* (cf. Pinder and Reiss 1986: Fig. 10.59D), but with the anterior band of shagreen not conspicuously heavier than the posterior; tergum IV (Fig. 45), tergum VI (Fig. 46), and tergum VIII (Fig. 47). Pedes spurii B on terga I and II. Tergum II hooks 69–72 in a single row. Anal lobe with 27–42 swim fringe setae.

DIAGNOSIS AND DISCUSSION.—The male of this species is only weakly separated, based on color features, from the closely related *P. obediens* (Johannsen) (Townes 1945). These 2 species may prove ultimately to be conspecific when more material is available for examination. The pupa is very similar to *P. flavipes* but differs in having a more heavily tuberculate cephalothorax.

ECOLOGY.—Grodhaus (1987) took *Phaenopsectra profusa* from temporary pools in California and suggested that the species maintains itself in permanent waters and opportunistically invades temporary pools, since it also has been found in rice fields, reservoirs, and sewage lagoons. Ruse et al. (unpublished data) collected adults of this species in the upper Arkansas River of Colorado at elevations ranging from 1431 to 2944 m. Its rarity in the Colorado River in Grand Canyon bespeaks a paucity of lentic habitats, principally small backwater and side pools.

DISTRIBUTION.—Washington to Montana south to California and New Mexico.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 Lex, Pex, ♂, river mi 31.8, 876 m elev; 1 P♂, 3 LL, river mi 53.0, 847 m elev; 2 LL, river mi 225.0, 411 m elev.

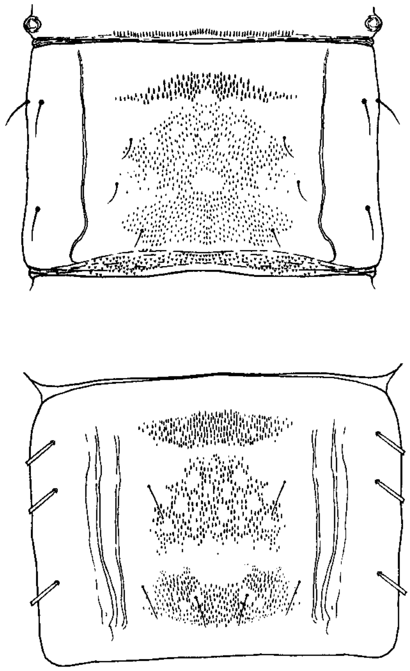
Polypedilum (Tripodura) obelos
Sublette & Sasa

(Figs. 49–52)

Polypedilum (Tribelos) obelos Sublette & Sasa 1994:50; type locality, Lavaderos, Guatemala, male and female.

PUPA.—Total length 4.67, 5.52 mm (2).

Cephalothorax: Frontal apotome without tubercles (Fig. 48); frontal setal length 62 µm. Thoracic horn with 3 posterior branches and about 5 anterior branches, similar to that of



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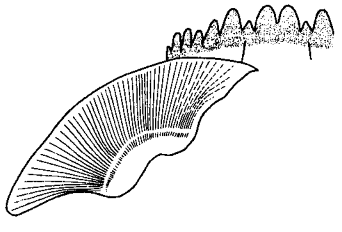

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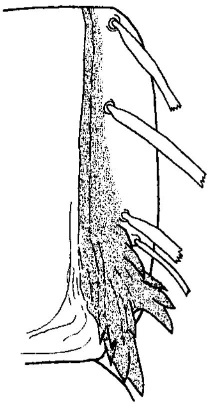

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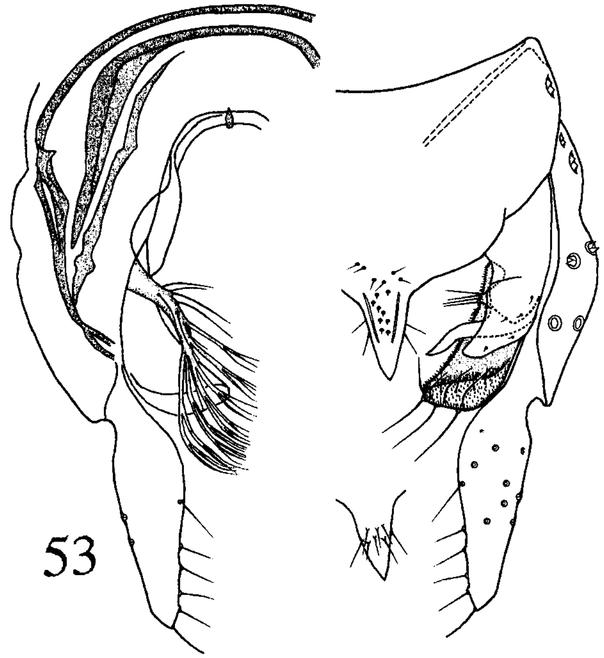

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Figs. 49–53. *Polypedilum (Polypedilum) obelos.* Pupa: 49, terga III (above) and VI (below) shagreen and chaetotaxy; 50, posterolateral spur of tergum VIII. Larva: 51, antenna; 52, mentum and ventromental plate. *Cladotanytarsus (Cladotanytarsus) marki.* Male: 53, genitalia.

Polypedilum (Tripodura) epomis Sublette and Sasa (Sublette and Sasa 1994: Fig. 170). Precorneal setae 2, 52 µm in length, subequal. Median suture with moderate tubercles anteriorly on either side; posteriorly becoming weakly rugose. Dorsocentral setae minute, anteriorly with DcS_1 and DcS_2 contiguous and posteriorly with DcS_3 and DcS_4 the same. Bacatiform papillae and nasiform tubercles lacking.

Abdomen: Abdomen length 3.48, 4.15 mm (2). Tergum I with weak reticulation; PSB I and II present. T II apical hooks 54, 62 (2). PSA present on S IV–VI. Terga III–V shagreen as in Figure 49; T VI with weaker shagreen so that the anterior, medial, and posterior transverse bands are separate. Intersegmental membrane II/IV and IV/V with weak shagreen (Fig. 49). Lateral abdominal setae: II–IV with 3 filiform setae, V–VI with 3 lamellate setae, and VII–VIII with 4. Posterolateral spur of T VIII (Fig. 50). Anal lobe with 38, 42 (2) fringe setae.

LARVA.—Head capsule yellowish except for tips of mandibles, mentum, and occipital ring. Ventral head length 160 µm (1).

Antenna (Fig. 51): Length 90 µm (1); AR 0.80; lauterborn organs large, extending past 3rd segment.

Head and mouthparts (Fig. 52): Mentum with 16 teeth, similar to other members of the genus. Ventromental plate (Fig. 52) with 40–61 fine striae. Premandible with a conspicuous brush, 2 apical teeth, and 1 basal shelf-like tooth. Mandible length 114 µm; seta subdentalis attenuate, down-curved at tip, extending past the basal tooth, similar to that illustrated by Pinder and Reiss (1983: Fig. 10.60C); subapical tooth heavy, scarcely exceeded in length by the apical tooth; mola with 1 very weak denticle; seta interna with numerous fine branches, major branches not discernible. Pecten epipharyngis, chaetulae laterales, ungula, and basal sclerite similar to that of *P. (Tripodura) griseopunctatus* (Malloch) (Soponis and Simpson 1992), but with 5 denticles in each of the lateral plates of the pecten epipharyngis and 6 chatulae laterales on each side; S I and S II simple, fimbriate. Chaetae 5 on each side, weakly fimbriate. Spinulae 2. Lacinial chaetae of maxilla 3, the most anterior one heaviest, reaching to midline of head; 2nd about as long but narrower, and 3rd greatly reduced. Maxillary palpus slightly longer than wide, with at least 7 apical sensillae. Dorsal labral sclerites obscured.

Body: Anterior parapods separate, mostly with pectinate claws. Procerci each with 6 terminal setae and 2 anterior setae; L/W of procercus about 1.0. Claws of anal parapod yellow, simple.

DIAGNOSIS.—This species closely resembles *P. (Tripodura) pterosopilus* Townes in wing features but differs from that species in having the basal dark spot in cell R_5 clearly separated from the r-m crossvein and having spots along the anal margin broader and heavier (cf. Sublette and Sasa 1994: Fig. 181). Male genitalia anal point is longer and more lanceolate (cf. Sublette and Sasa 1994: Fig. 182) than in *P. pterosopilus* (Townes 1945: Fig. 32). The genitalia of *P. (Tripodura) labeculosum* (Mitchell) are more similar to this species (cf. Sublette 1960: Fig. 1C), but the wing spots of *P. labeculosum* are distinctively different (cf. Townes 1945: Fig. 211). Immature stages in this genus are still inadequately known. Of the known southwestern larvae this species most closely resembles *P. labeculosum* in having antennal segments 3–5 about equal to segment 2, ventromental plates finely striate (30–47 striae), head capsule largely pale, and posterior margin of the ventromental plate not strongly sinuate. This species differs, however, in having the 5th antennal segment minute and scarcely distinguishable. The pupa differs from most other southwestern species in having the anterior band of shagreen only slightly greater density than the middle and posterior bands of T II–VI. This, coupled with the heavy, somewhat divided, posterolateral spur of T VIII, presents a unique appearance among the southwestern *Polypedilum*.

DISCUSSION AND ECOLOGY.—The presence of *P. obelos* in Grand Canyon represents the northernmost occurrence of this recently described Neotropical species. The related *P. labeculosum* and *P. pterosopilus* also represent probable Neotropical forms with range extensions into the southwestern United States.

DISTRIBUTION.—Guatemala, Arizona, New Mexico

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂ and Pex, river mi 61.0, 663 m elev; 1 ♂ and Pex, 1 Lex, river mi 166.0, 646 m elev.

Polypedilum (Tripodura) apicatum Townes

Polypedilum (Tripodura) apicatum Townes 1945:39; type locality, Las Vegas Hot Springs, NM; Boesel 1985:258, review; Oliver et al. 1990:52, catalog, distribution.

DIAGNOSIS AND DISCUSSION.—Features of the male genitalia and the characteristic spotted wing are distinctive (cf. Townes 1945: Figs. 31, 207).

ECOLOGY.—This species is found at low elevations in the Southwest and has been collected in desert springs.

DISTRIBUTION.—California to Colorado and New Mexico; Illinois.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 1 ♂, river mi 164.5, 533 m elev; 1 ♂, river mi 166.5, 532 m elev.

Tribe Tanytarsini

Cladotanytarsus marki
Sublette, new species

(Fig. 53)

HOLOTYPE MALE.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, river mi 174.3, 518 m elev, UV trap, LES (CAS).

Coloration: Head, antepronotum, thoracic vittae, preepisternum, a spot on the pleura, and postnotum blackish brown; humeral, prescutellar, and pleural areas and scutellum yellowish; legs and abdomen dark.

Head: Antenna with 13 flagellomeres. Antennal ratio 0.72 (0.60–0.64; 3). Palpal proportions 23:78:78:125 µm. Eyes reniform; ocular ratio 0.71 (0.64–0.72; 3). Clypeus truncate triangular, width at base 0.65 of width of antennal pedicel; with 8 (8–10; 4) setae. Temporal setae 9 (8–9; 4), in a single row, reaching to over halfway to midline of the head.

Thorax: Antepronotum triangular, evanescent dorsally. Thoracic chaetotaxy: lateral antepronotals lacking; dorsocentrals 7 (5–6; 4), in a single row; acrostichials 5 (5–6; 4), partially in 2 rows; prealars 1(1; 4); supra-alars lacking; scutellars 2 (2–4; 3), in a single row.

Wing: Membrane with sparse macrotrichia at the tip; R_{4+5} ends very slightly proximal to apex of M_{1+2}. R_{2+3} ends at 0.65 (0.56–0.65; 4) of the distance between apex of R_1 and R_{4+5}. Venarum ratio 1.25 (1.27–1.31; 5). Wing length 1.26 (1.18–1.45; 4) mm. Wing vein setae: R 10 (7–10; 4), R_{4+5} 4 (1–5; 4), M_{1+2} 15 (7–15; 4).

Legs: Foretibial spine length 12 µm; middle tibial spurs subequal, lengths 10 µm; hind tibial spur lengths 10/8 µm. Pulvilli vestigial. Leg ratios: P I 1.58 (1.89–1.97; 3); P II 0.53 (0.53–0.56; 3); P III 0.65 (0.61–0.67; 3). Sensilla chaetica P II 2 (2; 3).

Abdomen: Genitalia (Fig. 53). Ninth tergum with 6 (3–11; 4) setae; ventral anal point setae extending slightly beyond middle of anal point (Fig. 53, inset). Gc/Gs ratio 1.43 (1.26–1.45; 4).

DIAGNOSIS AND DISCUSSION.—The medially concave inferior volsella separates this species from all described Nearctic *Cladotanytarsus* except *C. daviesi* Bilyj and *C. pinnaticornis* Bilyj. In those species the anal point spinulae have multiple points at the tip with the spinulae and 9th tergum setae distinctly separated in both size and shape, while *C. marki* has simple tips so that the spinulae grade into the 9th tergum setae.

PARATYPES.—AZ: Coconino Co., Colorado River, Grand Canyon National Park, 1 ♂, river mi 108.5, 663 m elev, 26-XI-91, TCM; 4 ♂♂, collected with the holotype ♂ (CAS, USNM).

This species is dedicated to the son of JES, Dr. J. Mark Sublette, who has devoted many hours in the field in pursuit of elusive midges.

ECOLOGY.—This species has been collected in cold-stenothermic conditions in both steep, narrow, bedrock-constrained and wider reaches of the mainstream Colorado River.

DISTRIBUTION.—This species has been collected only in the lower half of the Colorado River corridor in Grand Canyon, Arizona.

Micropsectra sp.

DIAGNOSIS AND DISCUSSION.—A single female pupal exuvium was taken at Lees Ferry on 30 December 1990, but the lack of knowledge on female pupal morphology prevented identification to the species level.

ECOLOGY AND DISTRIBUTION.—The most common southwestern *Micropsectra* is *M. nigripila* (Johannsen), which has a very broad ecological tolerance, occurring in a variety of flowing water.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado R, 1 ♀ Pex, river mile 0.0, 950 m elev, 30-XII-90.

Rheotanytarsus hamatus
Sublette and Sasa

Rheotanytarsus hamatus Sublette and Sasa 1994:52; type locality, Rincon, Guatemala.

DIAGNOSIS AND DISCUSSION.—The genitalia of the males available are in rather poor condition; however, the strongly hooked gonostylus, short medial volsellus, and distinctively shaped superior volsellus are clearly visible (cf.

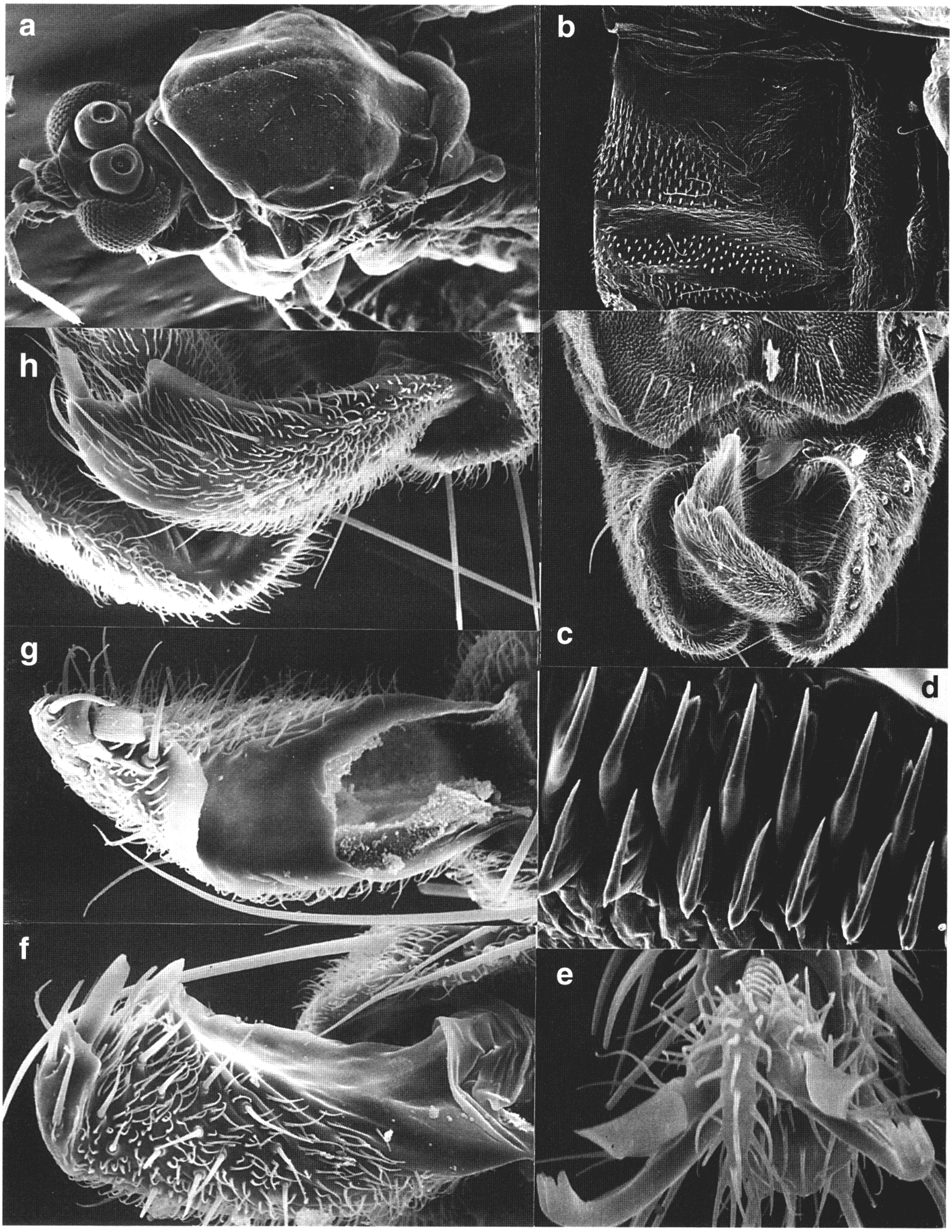

Fig. 54. *Cricotopus (Cricotopus) blinni,* scanning electron micrographs (clockwise from top left): (a) male, head and thorax (dorsolateral view); (b) pupa, tergum III (lateral view); (c) male, genitalia; (d) pupa, recurved hooks of tergum II; (e) male, claws and associated structures; (f) male, gonostylus (ventral); (g) gonostylus (medial); (h) gonostylus (lateral).

Fig. 55. *Cricotopus (Cricotopus) blinni*, scanning electron micrographs (clockwise from top left). Larva: (a) mandible (3-piece collage); (b) head (ventral view); (c) anterior parapods; (d) maxillary palpus apex; (e) maxilla.

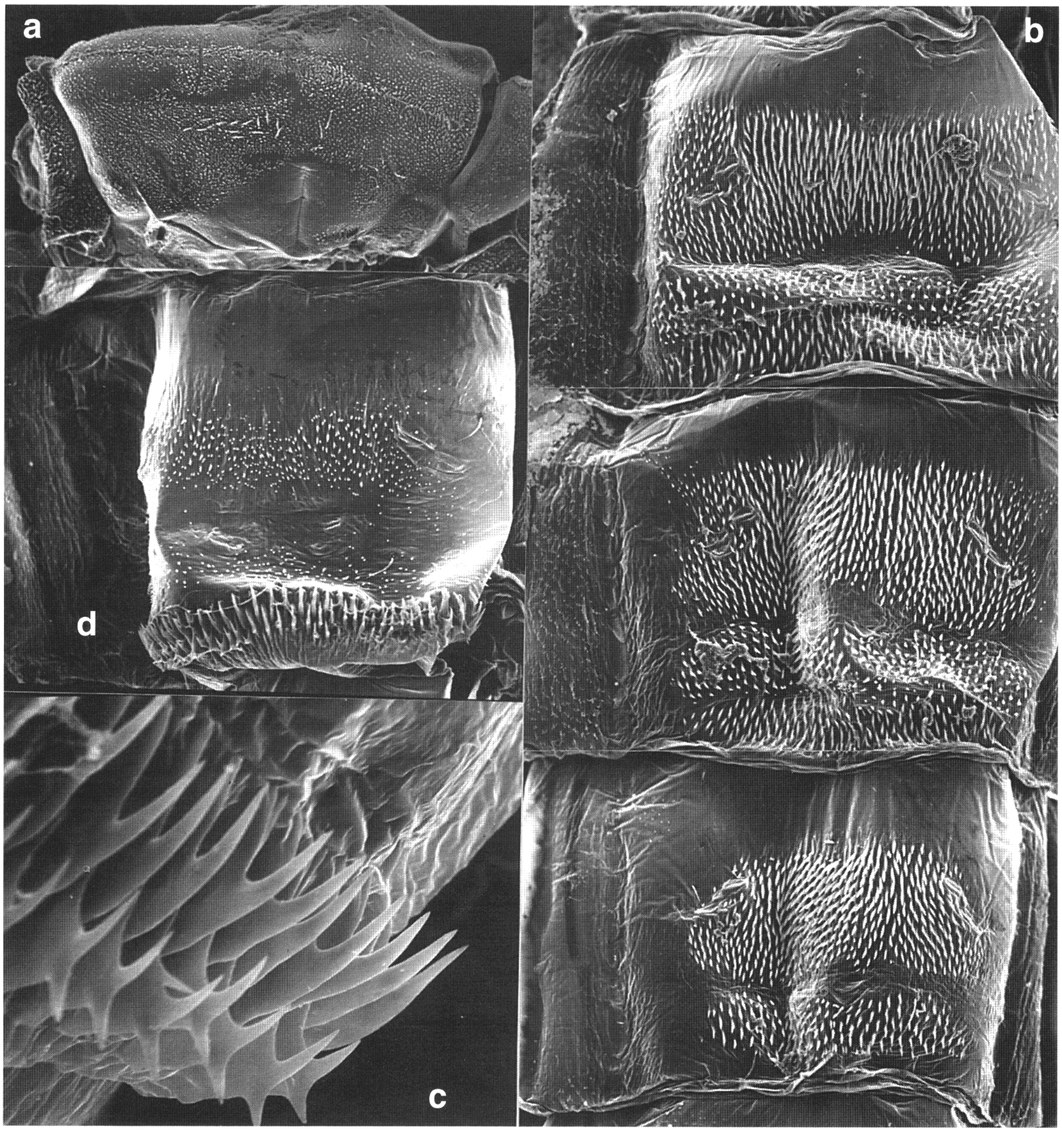

Fig. 56. *Cricotopus (Cricotopus) globistylus*, scanning electron micrographs (clockwise from top left). Male: (a) thorax (dorsolateral view). Pupa: (b) terga IV–VI (3-piece collage); (c) recurved hooks of tergum II; (d) tergum II.

Sublette and Sasa 1994: Fig. 188), thus providing a positive identification.

ECOLOGY AND DISTRIBUTION.—In Arizona this species has been collected in cold-stenothermic conditions in the Colorado River just below the Paria River.

MATERIAL EXAMINED.—AZ: Coconino Co., Grand Canyon National Park, Colorado River, 4 ♂, river mi 133.5, 610 m elev.

SUMMARY

The chironomid fauna of the Colorado River in Grand Canyon is depauperate in comparison with other North American rivers. Our sample of nearly 1500 larval, pupal, and adult chironomid specimens included 38 species in 23 genera and 4 subfamilies. The fauna was dominated by 23 species in the subfamily

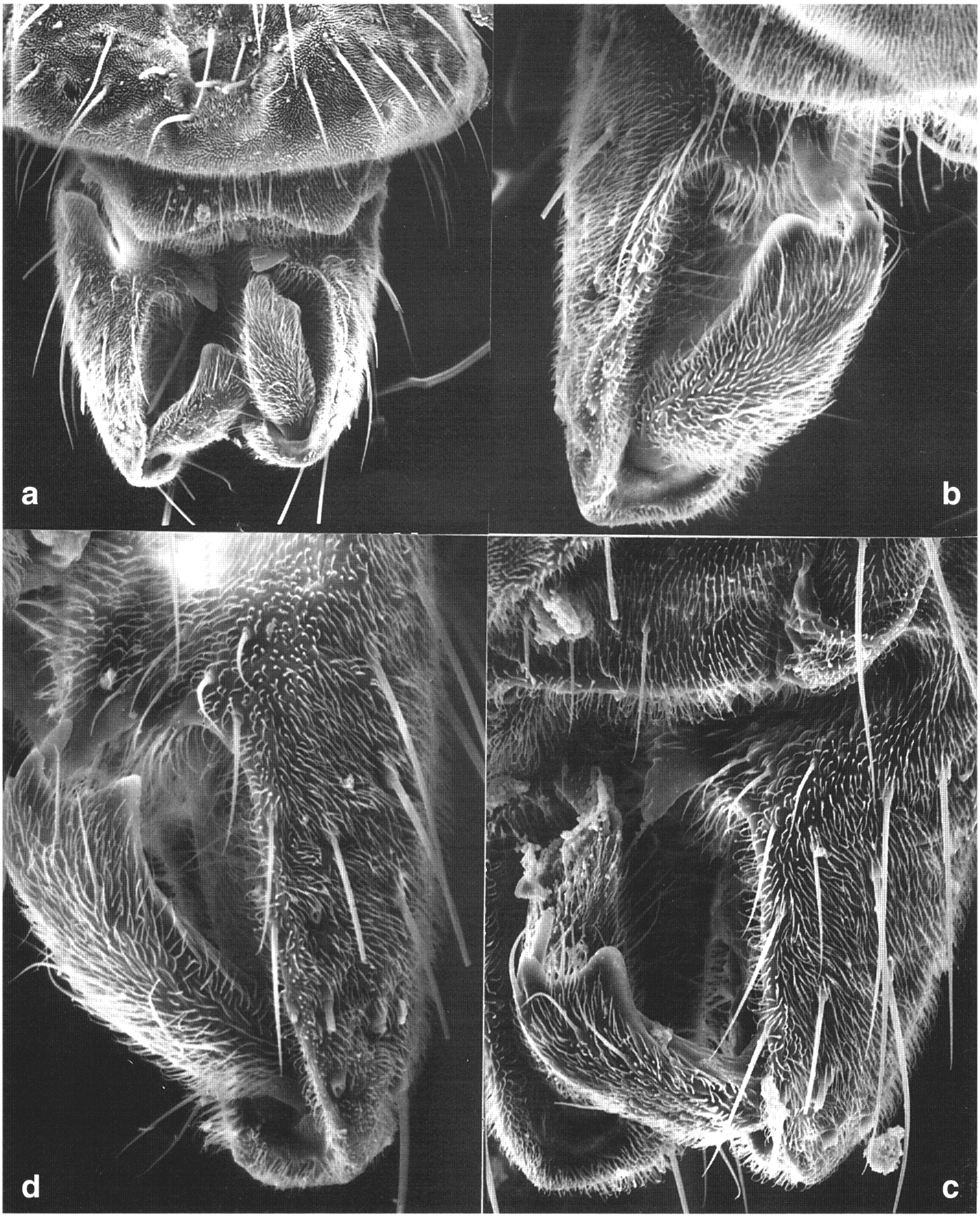

Fig. 57. *Cricotopus (Cricotopus) herrmanni,* scanning electron micrographs (clockwise from top left). Male: (a) genitalia; (b–d) gonostylus, positional variation.

Orthocladiinae, with *Cricotopus annulator* > *C. globistylus* > *Eukiefferiella claripennis* > *Orthocladius rivicola* > *Tvetenia vitracies*. *Chironomus* spp. (subfamily Chironominae) were regularly encountered in low densities in pool habitats floored with fine sediment. Twelve chironomine species were collected overall. *Procladius bellus*, *Paracladius conversus*, *Chironomus decorus*, *C.* sp. 1, and *C.* sp. 2 were collected only in the headwaters of Lake Mead.

Stevens et al. (1998) present a synthesis and summary of the Colorado River chironomid assemblage from the data presented here.

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CHIRONOMIDAE (DIPTERA) OF THE COLORADO RIVER, GRAND CANYON, ARIZONA, USA, II: FACTORS INFLUENCING DISTRIBUTION

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ABSTRACT.—Biogeographic, flow regulation (water clarity and temperature), and temporal influences affect the composition of the chironomid midge assemblage in the Colorado River between Glen Canyon Dam and Lake Mead. This assemblage is dominated by euryecious Nearctic and Holarctic orthocladine taxa (23 of 38 total species, total weighted relative abundance [WRA] = 0.972) and includes a minor Neotropical component. Chironomid species richness increases over distance downstream from the dam, and dominance shifts across 3 turbidity segments. Eleven species occur in the cold-stenothermic clearwater (CW) segment between the dam and the 1st perennial tributary (the Paria River, 26 km from the dam). Chironomid diversity increases from 18 to 24 species in the variably turbid (VT) and usually turbid (UT) segments downstream, respectively. Total *Cricotopus* spp. WRA is negatively correlated with distance (turbidity), while total Chironominae WRA shows the opposite pattern. In contrast to chironomid diversity, species density decreases from 0.42 species/km in the CW segment to 0.19 and 0.08 species/km in the VT and UT segments, respectively. Seasonal dominance shifts slightly from orthocladine *Eukiefferiella* spp. in winter (WRA = 0.101) to *Cricotopus* spp. (WRA = 0.165) in summer. Total WRA is lowest in spring (0.191). The assemblage is depauperate compared with other western rivers and has changed over post-dam time.

Key words: biodiversity, biogeography, Chironomidae, Colorado River, community, flow regulation, Glen Canyon Dam, Grand Canyon, serial discontinuity concept.

Chironomid midges play important roles in both aquatic and terrestrial food webs in river ecosystems. The Colorado River is one of the most thoroughly regulated American rivers (Hirsch et al. 1990), and chironomids are abundant or dominant taxa in many segments (Pearson 1967, Rader and Ward 1988, Wolz and Shiozawa 1995, Stevens et al. 1997). Virtually no pre-impoundment mainstream benthic data were collected (Blinn and Cole 1991). Following completion of Glen Canyon Dam in 1963, Stone and Rathbun (1967 unpublished) documented rapid changes in benthic macrophyte distribution at Lees Ferry, but reported the presence of only a single group of chironomids: ooze-dwelling "bloodworms" (Chironominae, probably *Chironomus* spp.). Sublette et al. (1998) identify 38 species of chironomids from the post-dam Colorado River in Glen and Grand canyons and discuss their autecology. These riverine Chironomidae link aquatic and terrestrial trophic components in Grand Canyon (Angradi 1994, Angradi and Kubly 1994a, 1994b, Blinn et al. 1995).

The Colorado River chironomid assemblage is influenced by biogeography (Sublette et al. 1998) as well as temporal and environmental factors, including flow regulation. However, detailed distributional data on individual chironomid species are rare, and phenology is well documented for rather few species. Hofnecht (1981) attributed low macroinvertebrate abundance in Grand Canyon tributary mouths to cold-stenothermic and fluctuating mainstream flows. Stevens et al. (1997) report that riffle and pool habitats in the clearwater segment immediately downstream from the dam support equally high densities of chironomid larvae in dense beds of the benthic alga *Cladophora glomerata*. In contrast, cobble bars in more turbid downstream segments support substantially greater chironomid abundance than do mainstream pool habitats. Chironomid species richness is low downstream from Glen Canyon Dam (Sublette et al. 1998), but other factors influencing diversity, such as seasonal phenology and impoundment impacts on water clarity, have not been analyzed.

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In this paper we synthesize taxonomic and ecological data of Sublette et al. (1998) to describe factors influencing the chironomid assemblage of the Colorado River between Glen Canyon Dam and Lake Mead. We use data from preserved pharate and adult chironomid specimens collected from 1974 through 1991 to describe biogeography, spatial and temporal distribution, and influences of flow regulation on this assemblage. Our results provide the first quantitative description of the chironomid assemblage in this portion of the Colorado River and establish a baseline for monitoring future change in these assemblages.

METHODS AND MATERIALS

Study Area

The channel of the Colorado River between Glen Canyon Dam and Lake Mead is constrained by talus slopes and bedrock. The river descends from an elevation of 955 m to 370 m over its 472-km-long course through Sonoran and Mohave Desert terrain (Warren et al. 1982). By convention, distances along the river are measured from Lees Ferry (river km and mi 0, 25 km downstream from the dam; Sublette et al. 1998: Fig. 1). The pre-dam mean daily flow ranged from <100 to >2500 m^3/s (Howard and Dolan 1981), with a spring snowmelt peak flow, erratic summer flows, and low winter flows. Pre-impoundment flows transported more than 60×10^6 mt/yr of inorganic sediment (Andrews 1991), and undoubtedly much organic drift. Water temperatures ranged from 0°C in winter to ≥29.4°C at Lees Ferry in summer before completion of the dam. The river channel is constricted by debris fans at the confluences of >500 mostly ephemeral tributaries. Runs, riffles or rapids, pools, and backwaters are primary river habitats, and their distribution varies through 13 bedrock-defined reaches (Schmidt and Graf 1990, Stevens et al. 1995, 1997).

Completion of Glen Canyon Dam in 1963 reduced effects of regional climate on the Colorado River and altered chironomid habitat availability. The post-impoundment hydrograph has been characterized by large hourly, but relatively minor seasonal, flow variability (Howard and Dolan 1981, U.S. Bureau of Reclamation 1995). Between 1963 and 1991, hourly flow variation for hydroelectric power production created daily "tides" of ≥3 m that inundated or desiccated shoreline habitats (Blinn et al. 1995). Seasonal thermal variability has been replaced by cold-stenothermic (hypolimnetic) flow releases (8–9°C) at Lees Ferry, and water temperature increases to only 17°C at Diamond Creek (km 364, mi 226) in summer (Stevens et al. 1997). Stabilized flows permit widespread establishment of aquatic, wetland, and riparian vegetation (Stone and Rathbun 1967 unpublished, Turner and Karpiscak 1980, Johnson 1991, Stevens et al. 1995), which serve as chironomid habitat. Sediment retention in Lake Powell increases water clarity in lower Glen Canyon; however, the Paria River (km 1, mi 0.7), Little Colorado River (km 98, mi 61), and other tributaries supply exceptionally concentrated suspended sediment loads (Andrews 1991, Graf et al. 1991). These tributaries create 3 turbidity segments: the 26-km-long clearwater (CW) segment from the dam to the Paria River confluence, the variably turbid (VT) segment from the Paria River and Little Colorado River mouth, and the usually turbid (UT) segment (km 98 to km 386, mile 240). In addition, upper Lake Mead (ULM) constitutes a usually turbid, lacustrine segment from km 386 to km 442 (mi 278).

Field and Analytical Methods

We collected adult and pharate aquatic Diptera throughout the year in 1976–77 and 1989–92 by sweep-netting riparian vegetation (particularly *Salix exigua, Tamarix ramosissima,* and *Baccharis* spp.), white- and UV light-trapping, dip-netting, and larval rearing from benthic spot and quantitative samples (Sublette et al. 1998). Taxonomic determinations and descriptions follow Sublette et al. (1998), which also includes additional information on collection methods, locations of specimens, and taxonomy.

We conducted spatial and seasonal analyses using data from 1018 slide-mounted pharate and adult specimens from 212 samples collected throughout the study area by Stevens (1976) from 1974 to 1976, and from 1989 through 1992. Up to 10 specimens of visually apparent species from each sample were slide-mounted for identification. Twenty samples were collected from the CW segment, 76 from the VT segment, 113 from the UT segment, and 3 from the ULM segment. Because few samples were collected in the last segment, we pooled ULM data with UT data. We sampled

Chironomidae throughout the year, with 54 samples collected in winter (December–February), 62 in spring (March–May), 47 in summer (June–August), and 49 in autumn (September–November).

By weighting the relative abundance of each species in relation to the number of samples collected in each turbidity segment, we standardized spatial distribution of adult chironomids. Species density was calculated by dividing the number of species in a turbidity segment by segment length (km). Seasonal variation was standardized by weighting each species' relative abundance by the number of collections made each season.

RESULTS AND DISCUSSION

Composition

The chironomid fauna of the Colorado River in Grand Canyon is depauperate in comparison with other western rivers (e.g., Sublette and Sublette 1979, Wolz and Shiozawa 1995, Spindler 1996). Our collections include 38 species in 23 genera and 4 subfamilies (Table 1). The fauna is dominated by the Orthocladiinae (23 species), with 5 abundant species: *Cricotopus annulator* > *Cricotopus globistylus* > *Eukiefferiella claripennis* > *Orthocladius rivicola* > *Tvetenia vitracies*. The fauna includes 12 Chironominae species, with *Chironomus* spp. regularly found in low densities in pool and backwater habitats floored with fine sand or silt, and with *Procladius bellus, Paracladius conversus, Chironomus decorus, C.* sp. 1, and *C.* sp. 2 collected only in the ULM segment.

Spindler (1996) reports at least 43 chironomid taxa in 38 genera from 10 Grand Canyon tributary streams, adding 20 genera to our list, for a total of 43 genera in Grand Canyon. Thus, more chironomid species may exist in tributary streams than in the mainstream Colorado River. Cowley (1995 unpublished) reports 172 chironomid species or taxa in the highly regulated Rio Grande in New Mexico, 4.5 times as many species as we encountered in the Colorado River mainstream.

Biogeography

Nine of the 38 species collected in the mainstream Colorado River are Holarctic in distribution and are madicolous or aufwuchs feeders (Sublette et al. 1998). All are Orthocladiinae, and the other orthocladines in this system also probably share this feeding strategy. The Orthocladiinae are primarily cool- or coldwater taxa, and their dominance in the Colorado River is not surprising because the river is now a cold-stenothermic stream, and because proximity to cold, high-elevation habitats provides a regional species pool of potential colonists. In contrast, the subfamily Chironominae, which largely consists of warmwater species, is represented by low densities of *Chironomus utahensis* and *C. decorus* in fine-grained habitats. A small Neotropical component is represented by *Polypedilum obelos* and *Rheotanytarsus hamatus*, which previously had been reported only from Guatemala (Sublette and Sasa 1994).

The depauperate condition of the Grand Canyon midge fauna may be explained partially by biogeographic constraints. Ecological isolation within this large, canyon-bound, desert river may have restricted pre-impoundment chironomid colonization. Colonization may have been restricted by the distance from source areas and by large annual ranges of water and air temperatures. Also, the combination of frequent large floods and high suspended and bed-transported sediment loads may have reduced pre-impoundment ecological heterogeneity, and therefore diversity. Coffman (1989) reviewed chironomid diversity in 152 stream studies, concluding that stream size and biogeographic potential, as well as ecological heterogeneity, altitude, and latitude, influence chironomid diversity. He reported the greatest chironomid diversity in medium-sized streams. Thus, the large, isolated, flood-prone, seasonally warm pre-impoundment Colorado River simply may not have supported many chironomid species. Polhemus and Polhemus (1976) similarly attribute the depauperate condition of the aquatic and semiaquatic Hemiptera fauna in Grand Canyon to biogeographic isolation; however, this argument may not apply as strongly to the Chironomidae because of adult dispersal as "aerial plankton."

Spatial Distribution Within the Study Area

The chironomid assemblage changes over distance from Glen Canyon Dam, through increasingly more turbid segments (Table 1). The CW segment supports the highest reach total weighted relative abundance (WRA = 0.471). The CW assemblage is strongly dominated by Orthocladiinae (0.468), particularly

TABLE 1. Sample-weighted relative abundance of adult Grand Canyon Chironomidae in 3 turbidity segments of the Colorado River downstream from Glen Canyon Dam.

	Turbidity Segments			
Taxa	Clearwater ($n = 20$)	Variably turbid ($n = 76$)	Usually turbid ($n = 116$)	Total ($n = 212$)
TANYPODINAE				
Procladius bellus	0.000	0.000	0.001	0.001
DIAMESINAE				
Diamesia heteropus	0.000	0.001	0.000	0.001
ORTHOCLADIINAE				
Cardiocladius platypus	0.003	0.002	0.003	0.007
Cricotopus annulator	0.173	0.087	0.044	0.303
Cricotopus blinni	0.000	0.000	0.003	0.003
Cricotopus globistylus	0.181	0.003	0.001	0.185
Cricotopus herrmanni	0.000	0.005	0.001	0.006
Cricotopus infuscatus	0.000	0.000	0.006	0.006
Cricotopus trifacsia	0.003	0.008	0.012	0.023
Undet. *Cricotopus* sp.	0.000	0.001	0.001	0.001
Subtotal *Cricotopus* spp.	0.357	0.103	0.067	0.527
Eudactylocladius dubitatus	0.000	0.000	0.000	0.000
Eukiefferiella claripennis	0.038	0.039	0.060	0.137
Eukiefferiella coerulescens	0.009	0.004	0.006	0.018
Eukiefferiella ilkleyensis	0.012	0.028	0.016	0.055
Undet. *Eukiefferiella* sp.	0.000	0.002	0.009	0.011
Subtotal *Eukiefferiella* spp.	0.059	0.073	0.090	0.221
Undet. *Limnophyes* sp.	0.000	0.000	0.001	0.001
Metriocnemus stevensi	0.000	0.002	0.000	0.002
Orthocladius frigidus	0.000	0.000	0.000	0.000
Orthocladius lutipes	0.000	0.001	0.000	0.001
Orthocladius mallochi	0.000	0.000	0.001	0.001
Orthocladius rivicola	0.032	0.049	0.033	0.114
Undet. *Orthocladius* sp.	0.000	0.001	0.002	0.003
Subtotal *Orthocladius* spp.	0.032	0.051	0.035	0.118
Paracladius conversus	0.000	0.000	0.001	0.001
Parakiefferiella subaterrima	0.000	0.000	0.002	0.002
Parametriocnemus lundbeckii	0.000	0.000	0.001	0.001
Paraphaenocladius exagitans	0.000	0.001	0.000	0.001
Pseudosmittia nanseni	0.003	0.000	0.000	0.003
Undet. *Pseudosmittia* sp.	0.000	0.000	0.000	0.001
Tvetenia vitracies	0.015	0.042	0.032	0.089
Total Orthocladiinae	0.468	0.274	0.230	0.972
CHIRONOMINAE				
Chironomini				
Apedilum subcinctum	0.000	0.001	0.000	0.001
Chironomus decorus	0.000	0.000	0.003	0.003
Chironomus utahensis	0.003	0.002	0.000	0.004
Chironomus sp. 1	0.000	0.000	0.001	0.001
Chironomus sp. 2	0.000	0.000	0.001	0.001
Cyphonella gibbera	0.000	0.000	0.002	0.002
Phaenospectra profusa	0.000	0.000	0.001	0.002
Polypedilum apicatum	0.000	0.000	0.001	0.001
Polypedilum obelos	0.000	0.000	0.002	0.004
Undet. *Polypedilum* sp.	0.000	0.000	0.001	0.001
Tanytarsini				
Cladotanytarsus marki	0.000	0.000	0.006	0.006
Rheotanytarsus hamatus	0.000	0.000	0.003	0.003
Undet. *Micropsectra* sp.	0.000	0.000	0.000	0.000
Total Chironominae	0.003	0.006	0.018	0.027
GRAND TOTAL	0.471	0.281	0.248	1.000
TOTAL SPECIES RICHNESS	11	18	24	38
SPECIES DENSITY (species/km)	0.42	0.19	0.08	

Cricotopus (genus total WRA = 0.357), with *C. globistylus* (0.181) and *C. annulator* (0.173) most abundant. *Eukiefferiella* spp. (genus total WRA = 0.059), particularly *E. claripennis* (0.038), and 8 other species are subdominant in the CW segment. The river floor substrata in the CW segment has changed from primarily sand to primarily cobble in post-dam time (Howard and Dolan 1981). Benthic cobbles have been colonized by *Cladophora glomerata*, a filamentous green alga that supports abundant epiphytic diatoms on which chironomid larvae feed (Hardwick et al. 1992, Blinn et al. 1995), and more recently by additional macrophyte taxa.

Downstream from the confluence of the small but extremely turbid Paria River the chironomid assemblage undergoes a 3.5-fold reduction in total WRA of *Cricotopus* spp., with low-density co-dominance by *C. annulator*, *Eukiefferiella claripennis*, *Orthocladius rivicola*, and *Tvetenia vitracies* (Table 1). Low chironomid standing stock biomass (Stevens et al. 1997), low WRA values (<0.061), and continued co-dominance of these species (except *Tvetenia vitracies*) also characterize the UT segment in lower Grand Canyon. Chironomid diversity increases from the CW (11 species) to the VT segment (18 species) to the UT (24 species); however, species density decreases from 0.43 spp./km to 0.19 spp./km and 0.08 spp./km through these turbidity segments, respectively.

Similarity with Other Western Rivers

Similarity between the Grand Canyon chironomid assemblage and that in other portions of the Colorado River or in other western rivers is negatively related to distance from our study area. Eighteen of 38 chironomid genera reported by Spindler (1996) in Grand Canyon tributaries also occur in the Colorado River mainstream; however, additional sampling of other tributaries, seeps and springs, and canyon rim wetlands is needed to provide a more complete understanding of chironomid diversity in Grand Canyon.

The post-impoundment Colorado River in Grand Canyon supports habitats and chironomid species that also occur in the upper and middle Green River, 600 km upstream. Wolz and Shiozawa (1995) report 19 genera of Chironomidae in Ouray National Wildlife Refuge, Utah, in low-velocity environments, including *Chironomus, Cricotopus, Cryptochironomus, Polypedilum, Procladius, Tanypus,* and *Tanytarsus*. Chironomid density there ranges up to 31,125/m^2 in river backwaters, an order of magnitude greater than that in the mainstream. The Grand Canyon portion of the Colorado River also contains numerous backwaters; however, steep gradients and swift currents limit fine-sediment deposition. Consequently, chironomid densities (primarily *Chironomus* spp.) in contemporary Grand Canyon backwaters are typically <1000/m^2 (Stevens unpublished data). Chironomids in the Colorado River in Grand Canyon are often more concentrated in cobble bar habitats, which are relatively rare on the sand-floored Green River. Habitat availability and biogeograhic constraints are probably responsible for assemblage variation between the 2 study areas.

Cowley (1995 unpublished) describes chironomid assemblages in the Rio Grande in New Mexico using Ward's (1963) clustering algorithm. He reports a total of 172 species that can be categorized into 3 distinct clusters. The 1st cluster includes 19 "widespread species," of which 8 also occur in Grand Canyon. His 2nd cluster comprises cold, cleanwater species and shares 9 species in common with the Grand Canyon fauna. His 3rd cluster includes species of lower elevations and shares 7 species in common with the Grand Canyon fauna. Five of the remaining 13 species from Grand Canyon could not be identified to species level because of poor preservation but probably also occur in New Mexico as members of the 3rd cluster. Thus, at least 24 (14%) of the Rio Grande chironomids co-occur on the Colorado River mainstream, a relatively small amount of faunal overlap when compared to the compositional overlap at other locations within the Colorado River basin.

Flow Regulation Impacts

The serial discontinuity concept (SDC; Ward and Stanford 1983) predicts that macroinvertebrate diversity decreases following impoundment, but increases with distance downstream from large dams on large rivers. The depauperate midge diversity in Grand Canyon generally supports the predictions of that model and reflects impoundment influences of cold-stenothermic release temperatures and fluctuating flows (Blinn et al. 1995). Water temperature during prepupal and pupal development influences chironomid emergence, at least for arctic lentic chironomids (Danks and Oliver 1972, Welch 1973, Butler 1980), and seasonal warming cues larval development (Ward and Stanford 1982). Although the CW segment supports extremely high benthic standing biomass, only those species capable of tolerating cold-stenothermic conditions can persist there. Taxa we report there are primarily euryecious Nearctic or Holarctic Orthocladiinae, with relatively large body sizes (e.g., *Cricotopus* spp.). The great abundance but low diversity of chironomid species in the CW segment reflects the large standing stock biomass of epiphytic algae and relatively high productivity (Blinn et al. 1995, Stevens et al. 1997). The negative correlation between chironomid species density (as the number of species/km) and distance downstream does not follow SDC predictions, suggesting that the SDC may be refined by additional study of species/area biogeographic influences.

Potential niche diversity (as the range of available types of niches) increases downstream in Grand Canyon through increased seasonal variation in water temperature, increased size and abundance of backwaters in wide reaches, variation in benthic algal composition, increased organic drift from tributaries and allocthonous sources, and increased variability of other ecological gradients (Schmidt and Graf 1990, Shannon et al. 1996). Dominance shifts from a lower diversity of larger-bodied *Cricotopus* spp. in the upstream clearwater segment to an assemblage dominated by smaller-bodied madicolous taxa (e.g., *Eukiefferiella* spp.), with lower abundance and species density in downstream reaches. This pattern is at least partially attributable to turbidity (distance)-related reduction in aquatic macrophyte standing biomass, which provides abundant food and habitat upstream. Dam impacts on temperature limit invertebrate diversity, while water clarity limits benthic standing biomass in this system.

Cowley (1995 unpublished) examines the similarity of chironomid assemblages in regulated and unregulated reaches of the Rio Grande in New Mexico, reporting 5 groups of sites (4 clusters and 1 outlier site). His least perturbed (outlier) site on the Chama River supports 76 species, of which 22 occur only at that site. One group of sites on the Chama River contains 2 stations downstream from dams. Those sites have high mean diversity (41 species/site) but, on average, only 4 unique species per site. A 2nd cluster, representing moderate to low water quality, has a mean of only 25 species with a mean of only 2 unique species per site. The diversity pattern in this cluster resembles that in our study area; however, Colorado River water quality is relatively high. In contrast to our study, Cowley reports that Chama River chironomid diversity is negatively correlated with distance downstream from Abiquiu Dam, with highest midge diversity at the coldest station just downstream from the dam.

Sublette and Sublette (1979) compare the Chironomidae from regulated and unregulated sites on the Navajo River above Navajo Dam and on the San Juan River at Farmington, New Mexico, about 65 km downstream from the dam. They report 67 species at the above-dam site and 56 below the dam, just downstream from the Animas River confluence at Farmington, New Mexico. The above-dam site is comparable to Cowley's least perturbed site on the Chama River, while the assemblage below the dam resembles his 1st cluster on the Chama River. The influence of that relatively large tributary restores water temperature variability and may explain the similarity of chironomid diversity above and below the impoundment. No tributary entering the Grand Canyon portion of the Colorado River is large enough to restore mainstream temperature, and flow regulation impacts on temperature persist throughout the entire study area (Stevens et al. 1997).

Hourly flow fluctuations in Grand Canyon affect chironomid diversity by regularly inundating or desiccating large portions of the shoreline (Blinn et al. 1995). We observed, but did not quantify, rapid emergence of *Cricotopus* and other chironomids from *Cladophora glomerata* beds exposed by fluctuating flows.

Temporal Variation

The chironomid assemblage in Grand Canyon changes only slightly between seasons but has shifted over post-dam time (Table 2). Chironomid diversity increases from 17 species in winter and spring to 22 and 21 species in summer and autumn, respectively. Spring, summer, and autumn assemblages are dominated by *Cricotopus* spp. (genus WRA = 0.076, 0.165, and 0.114, respectively), particularly *C. annulator*. Winter dominance shifts to *Eukiefferiella*

Table 2. Seasonal sample-weighted relative abundance of adult Grand Canyon Chironomidae downstream from Glen Canyon Dam: winter (December–February), spring (March–May), summer (June–August), autumn (September–November).

Taxa	Season				
	Winter (*n* = 54)	Spring (*n* = 62)	Summer (*n* = 47)	Autumn (*n* = 49)	Total (*n* = 212)
Tanypodinae					
Procladius bellus	0.000	0.000	0.001	0.000	0.001
Diamesinae					
Diamesia heteropus	0.000	0.000	0.000	0.001	0.001
Orthocladiinae					
Cardiocladius platypus	0.003	0.003	0.001	0.001	0.008
Cricotopus annulator	0.013	0.049	0.114	0.086	0.262
Cricotopus blinni	0.001	0.000	0.001	0.003	0.005
Cricotopus globistylus	0.011	0.017	0.030	0.009	0.067
Cricotopus herrmanni	0.000	0.007	0.000	0.000	0.007
Cricotopus infuscatus	0.003	0.001	0.006	0.002	0.011
Cricotopus trifacsia	0.006	0.003	0.014	0.014	0.036
Undet. *Cricotopus* sp.	0.000	0.001	0.001	0.000	0.002
Subtotal *Cricotopus* spp.	0.034	0.076	0.165	0.114	0.389
Eudactylocladius dubitatus	0.000	0.000	0.000	0.000	0.000
Eukiefferiella claripennis	0.058	0.041	0.021	0.055	0.175
Eukiefferiella coerulescens	0.008	0.005	0.002	0.003	0.018
Eukiefferiella ilkleyensis	0.023	0.021	0.019	0.005	0.067
Undet. *Eukiefferiella* sp.	0.012	0.003	0.003	0.002	0.020
Subtotal *Eukiefferiella* spp.	0.101	0.070	0.045	0.065	0.280
Undet. *Limnophyes* sp.	0.001	0.000	0.000	0.000	0.001
Metriocnemus stevensi	0.000	0.001	0.001	0.000	0.002
Orthocladius frigidus	0.000	0.000	0.000	0.000	0.000
Orthocladius lutipes	0.000	0.000	0.001	0.000	0.001
Orthocladius mallochi	0.000	0.001	0.000	0.000	0.001
Orthocladius rivicola	0.071	0.017	0.034	0.015	0.136
Undet. *Orthocladius* sp.	0.004	0.001	0.000	0.000	0.005
Subtotal *Orthocladius* spp.	0.075	0.018	0.035	0.015	0.143
Paracladius conversus	0.000	0.000	0.000	0.002	0.002
Parakiefferiella subaterrima	0.001	0.001	0.000	0.001	0.003
Parametriocnemus lundbeckii	0.000	0.000	0.001	0.000	0.001
Paraphaenocladius exagitans	0.000	0.000	0.000	0.001	0.001
Pseudosmittia nanseni	0.000	0.001	0.000	0.000	0.001
Undet. *Pseudosmittia* sp.	0.000	0.000	0.001	0.000	0.001
Tvetenia vitracies	0.033	0.021	0.007	0.060	0.120
Total Orthocladiinae	0.248	0.190	0.256	0.259	0.953
Chironominae					
Chironomini					
Apedilum subcinctum	0.000	0.000	0.000	0.001	0.001
Chironomus decorus	0.000	0.001	0.002	0.002	0.005
Chironomus utahensis	0.001	0.000	0.002	0.000	0.003
Chironomus sp. 1	0.000	0.000	0.000	0.002	0.002
Chironomus sp. 2	0.000	0.000	0.000	0.001	0.001
Cyphonella gibbera	0.002	0.000	0.001	0.000	0.003
Phaenospectra profusa	0.003	0.000	0.000	0.000	0.003
Polypedilum apicatum	0.000	0.000	0.001	0.001	0.002
Polypedilum obelos	0.006	0.000	0.000	0.000	0.006
Undet. *Polypedilum* sp.	0.001	0.000	0.001	0.000	0.002
Tanytarsini					
Cladotanytarsus marki	0.000	0.000	0.002	0.009	0.012
Undet. *Micropsectra* sp.	0.000	0.000	0.000	0.000	0.000
Rheotanytarsus hamatus	0.000	0.000	0.006	0.000	0.006
Total Chironominae	0.012	0.001	0.015	0.017	0.045
Grand Total	0.260	0.191	0.272	0.277	1.000
Total Species Richness	17	17	22	21	38

(genus WRA = 0.101), particularly *E. claripennis* (winter WRA = 0.058), and *Orthocladius* spp. (genus WRA = 0.075), especially *O. rivicola* (WRA = 0.071). Adult *Tvetenia vitracies* are common from autumn through spring (0.06–0.021) and rare in summer (0.007).

The pre-impoundment river was characterized by large late spring or early summer floods. If non-*Cricotopus* Orthocladiinae characterized the pre-impoundment river, their phenology may reflect avoidance of spring and summer floods, with oviposition on the descending, warming, or autumn limbs of the hydrograph. Increased environmental constancy (unithermal releases and reduced flooding disturbance) and a shift in benthic substrata from silt/sand to cobble (Howard and Dolan 1981) favor species that apparently do not require warming cues and may emerge throughout the year (e.g., some *Cricotopus* spp.). As some thermal and substrate conditions are restored over distance downstream, total Chironominae WRA increases from 0.003 to 0.018 (Table 1).

The Colorado River chironomid assemblage has changed during post-dam time. Stone and Rathbun (1967 unpublished) noted only "blood worms" (probably *Chironomus* spp.) among numerous aquatic invertebrate collections at Lees Ferry immediately after impoundment. Identification of 49 adult specimens collected by Stevens (1976) in 1975 at Lees Ferry reveals an assemblage dominated by small-bodied *Cladotanytarsus* sp., *Tvetenia vitracies,* and *Apedilum subcinctum,* a species not collected subsequently. A total of 14 species collected there from 1990 to 1992 show strong dominance by *Cricotopus* spp. This chironomid assemblage is likely to continue to change through time as colonization occurs from tributaries and riverside springs, as extinction occurs, and in response to dam management policies.

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