



THE *ISOPERLA* OF CALIFORNIA (PLECOPTERA: PERLODIDAE); LARVAL DESCRIPTIONS AND A KEY TO 17 WESTERN NEARCTIC SPECIES

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ABSTRACT

The male larvae of 17 western Nearctic species of the stonefly genus *Isoperla* Banks from California, Oregon, and Colorado were reared and confirmed studying everted male aedeagi. New maxilla characters are described for male larvae and used as primary characters in a larval species key. The larvae of two species, *I. fulva* Claassen and *I. roguensis* Szczytko & Stewart could not be separated and two species not currently known to occur in California, *I. muir* Szczytko & Stewart and *I. tilasqua* Szczytko & Stewart were included in the descriptions and key. *Isoperla karuk* Baumann & Lee is placed as a synonym of *I. roguensis* Szczytko & Stewart, and the larva of *I. baumanni* Szczytko & Stewart is correctly associated for the first time with the previously published description of *I. bifurcata* Szczytko & Stewart.

Keywords: larval species key, maxillae, lacinia, *Isoperla*, western Nearctic

INTRODUCTION

The Holarctic stonefly genus *Isoperla* includes over 150 species (DeWalt et al. 2011) and a revision of the eastern Nearctic species is currently in progress (S.W. Szczytko & B.C. Kondratieff, pers. com.). The western North American species were revised by Szczytko & Stewart (1979) who gave descriptions for 20 species. Later they added *Isoperla baumanni* Szczytko & Stewart, *Isoperla roguensis* Szczytko & Stewart (Szczytko & Stewart 1984) and *Isoperla decolorata* (Walker) (Szczytko & Stewart 2002) to this list. Subsequently, Bottorff (1990), Szczytko & Stewart (2004) and Baumann & Lee (2009) added four additional western North American species, respectively. Huntsman et al. (1999) reported *Isoperla transmarina* (Newman) from Wyoming and Kondratieff & Baumann (2002) reported *Isoperla marlynia* (Needham & Claassen) from Colorado bringing the total to 29 species with western North American distributions (Table 1). While studying the

16 *Isoperla* species thought to occur in California, a new synonym was determined, one larval species description was found to be misassociated, and the occurrence of *Isoperla fulva* Claassen in California was not confirmed.

The objectives of this study were to provide comparative mature male larval descriptions and a larval species key for California *Isoperla* and two other western Nearctic species from adjacent Oregon. Szczytko & Stewart (1979) provided a larval key for 12 western *Isoperla* species, of which only six were thought to occur in California (*Isoperla sordida* Banks was described from a female exuvia and not included in the key and *Isoperla acula* Jewett, *Isoperla adunca* Jewett, *Isoperla bifurcata* Szczytko & Stewart and *Isoperla tilasqua* Szczytko & Stewart larvae were unknown). They used the presence or absence of a transverse spinule row near the occiput as the first morphological character for separating species in their key. In this study, the occipital spinule band

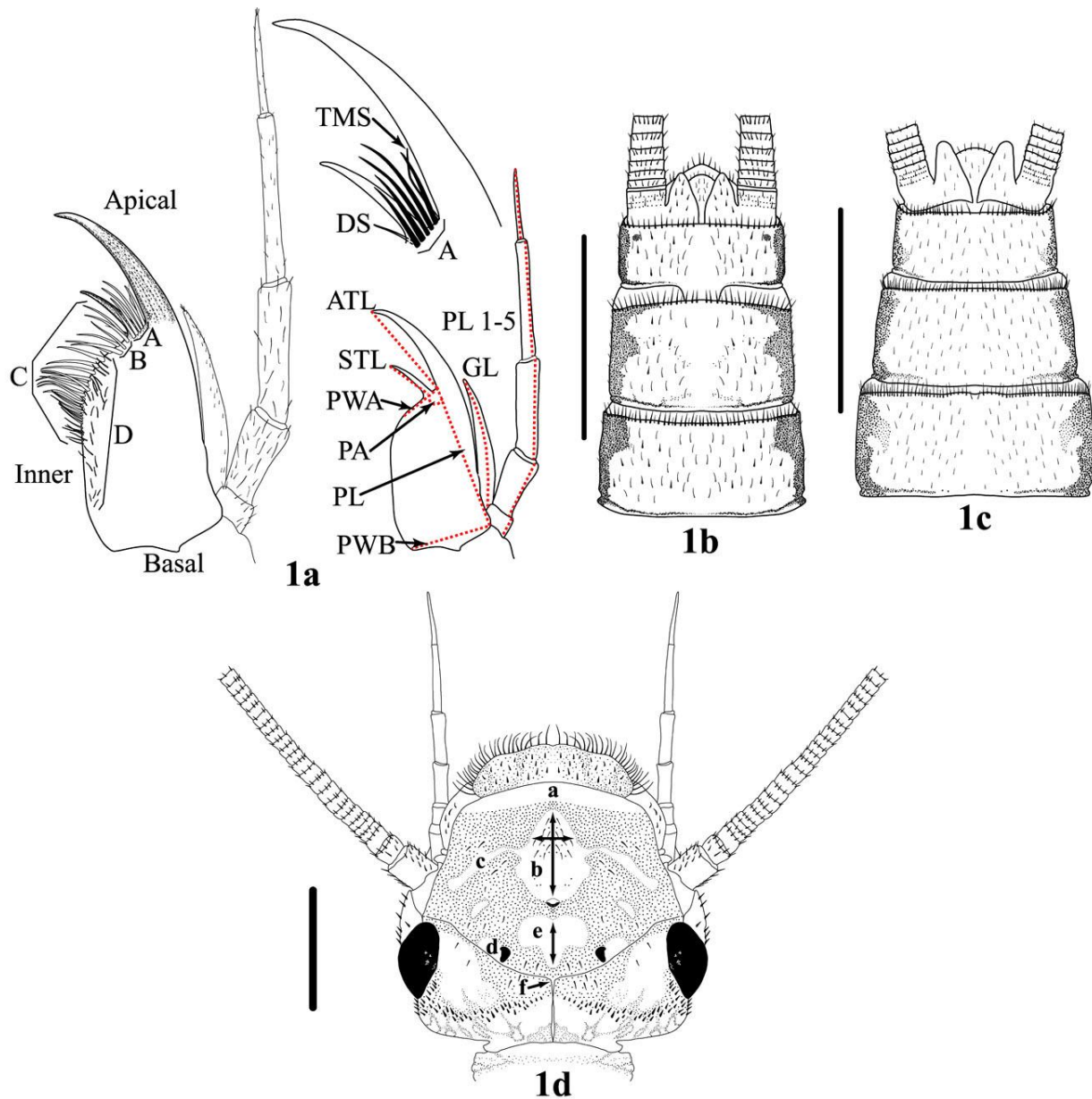


Fig. 1. *Isoperla baumannii* left ventral maxilla, abdominal sternites, and head, Domingo Spring, Plumas County, CA. 1a. Submarginal row groups (A) and (B), Marginal row (C), Ventral surface setae (D), Dorsal surface setae (DSS) not illustrated, Thin marginal seta (TMS), and Dorsal seta (DS) not included in submarginal row counts (Table 1). Maxilla measurements (red lines): Apical tooth length (ATL), Subapical tooth length (STL), Apical palm width (PWA), Palm angle (PA), Palm length (PL), Basal palm width (PWB), Galea length (GL), and Palp segment lengths (PL 1-5). 1b. Male and 1c. Female sterna. 1d. Dorsal head capsule: Anterior frontoclypeus area (a), Light M shaped pattern (b) and median longitudinal band (2 arrows), Lateral arms (c), Outer posterior ocellus light area (d), interocellar area (e) and length (arrow), and Epicranial suture (f). Bars = 1 mm.

was present in all species examined and maxilla characters were used to separate the species into morphological subgroups.

MATERIALS AND METHODS

All species in this study were reared and concise larval and adult correlations were determined. This was especially important for the larvae because some species had similar pigment patterns and most patterns were variable among and between species. In some streams, two to four species were collected from different benthic microhabitats or shared the same habitat but were separated by phenology.

Adults were collected in the field using a beating sheet and aspirator. Males were positively identified by everting the aedeagus in the lab. Rearing was accomplished by collecting larvae with a kick net, preserving some specimens immediately, and transporting others live in Styrofoam lined 250–500 ml Nalgene field rearing containers filled with stream water and held in ice chests. Laboratory rearing chambers (Styrofoam cups with plastic lids) held in a refrigerator were refilled with fresh stream water every other day, which was collected in 10–15 L containers when accessible by vehicle. If hiking to the site was required, then 250 ml Nalgene field rearing containers were held in a six-pack cooler with ice and stream water was transported in 1 L plastic bottles held in a backpack. The reared adult exuviae were associated with larvae collected from the same location by comparing the maxillae, leg setation and pigment patterns.

More than 1,200 adults were reared and preserved individually with their corresponding exuviae. The adult male aedeagi were everted under a dissecting microscope and fixed in near boiling water for approximately 2–3 seconds. In addition to fresh material, the following museums were especially helpful in allowing examination of *Isoperla* types and additional specimens: Norm D. Penny, California Academy of Science (CAS) and Oliver S. Flint Jr., Smithsonian National Museum of Natural History (NMNH). The Aquatic Bioassessment Lab – California Department of Fish & Game (ABL), provided specimens from its water quality studies throughout the state.

The left and right maxillae (lacinia, galea and maxillary palp) from 9–18 mature male larvae were

dissected and mounted ventral side up on microscope slides using CMCP-10 mounting media (Masters Company, Inc., Wood Dale, Illinois). The larval gender was determined by examining the distal eighth and ninth abdominal sternites (Figs. 1b–c). Female larvae were differentiated from males by the absence of setae along the median posterior margin of the eighth sternite (sometimes produced, usually margin with small invagination). The male larval abdominal ninth sternite is slightly longer. When numbers of preserved male larvae were low (*I. acula*, *Isoperla laucki* Baumann & Lee), only the left maxilla was mounted. Only two mature *I. tilasqua* male larvae were collected in Oregon for this study; and the lacinia of an additional eight male exuviae were used from rearing efforts in 2011. After mounting the maxillae, slides were placed in a Single-Wall Transite Oven (Blue M Electric Company, Blue Island, Illinois) at 48°C for a minimum of 1–2 hours which facilitated drying the media and clearing soft tissue inside sclerotized structures. Clearing allowed examination of the dorsal lacinia surface by focusing down through the ventral surface. Descriptions of maxilla characters were obtained using a compound microscope at magnifications ranging 40x–400x.

Photomicrographs were used for dorsal larval habitus, ventral maxillae, and lateral front right leg plates. Habitus and leg images were taken using a Zeiss Stemi SV6 dissecting microscope, intermediate phototube, 2.5x camera adapter, and Sony DSC S85 digital still camera. Scale bars measuring 1.0 mm were added by acquiring images of a millimeter scale and then transferred to larval images using Adobe Photoshop and Illustrator software. Maxillae images were taken using an Olympus CX41 compound microscope outfitted with a trinocular tube, video adapter and Lumenera Infinity2-2 high resolution (4.4 µm square pixels) microscopy camera. Lumenera Infinity Analyze software was used to capture images, place calibrated scale bars, and make maxillae length and angle measurements.

RESULTS

Szczytko & Stewart (1979) provided the first revision of the western Nearctic *Isoperla* which included 11 adult and six larval species thought to occur in California. They arranged the species into

Table 1. Systematic list of 29 western Nearctic *Isoperla* species and species complexes based upon characters of the male aedeagus and ovum. California species indicated with asterisk.

Species Complex	Western Nearctic Species	Adult Characters
<i>I. quinquepunctata</i>	<i>I. acula</i> Jewett 1962*	Aedeagus entirely membranous or with spinulae patches; ova uniformly punctuate, with or without elevated chorionic ridges
	<i>I. jewetti</i> Szczytko & Stewart 1979	
<i>I. longiseta</i> Banks 1906		
<i>I. mormona</i> Banks 1920*		
<i>I. quinquepunctata</i> (Banks 1902)*		
<i>I. phalerata</i>	<i>I. phalerata</i> Needham 1917	
	<i>I. pinta</i> Frison 1935*	
<i>I. sobria</i>	<i>I. baumanni</i> Szczytko & Stewart 1984*	
	Ovum unknown	
	<i>I. gravitans</i> (Needham & Claassen 1925)	
	Larva unknown	
	<i>I. miwok</i> Bortorff & Szczytko 1990*	
<i>I. marmorata</i>	<i>I. sobria</i> (Hagen 1874)*	
	<i>I. tilasqua</i> Szczytko & Stewart 1979	
	<i>I. fulva</i> Claassen 1937*	
	<i>I. karuk</i> Baumann & Lee 2009*	
	(= <i>I. roguensis</i> Szczytko & Stewart)	
<i>I. sordida</i>	<i>I. marmorata</i> Needham & Claassen 1925*	
	<i>I. roguensis</i> Szczytko & Stewart 1984*	
	<i>I. adunca</i> Jewett 1962*	
	<i>I. bifurcata</i> Szczytko & Stewart 1979*	
	<i>I. denningi</i> Jewett 1955*	
	<i>I. fusca</i> Needham & Claassen 1925	
Unassigned	<i>I. petersoni</i> Needham & Christenson 1927	
	<i>I. rainera</i> Jewett 1954	
	<i>I. sordida</i> Banks 1906*	
	<i>I. decolorata</i> (Walker 1852)	
	Ovum unknown	
	<i>I. katmaiensis</i> Szczytko & Stewart 1979	
Unassigned	<i>I. marlynia</i> (Needham & Claassen 1925)	
	<i>I. muir</i> Szczytko & Stewart 2004	
	<i>I. laucki</i> Baumann & Lee 2009*	
	<i>I. transmarina</i> (Newman 1838)	
	<i>I. marlynia</i> (Needham & Claassen 1925)	

five complexes based upon characters of the adult aedeagus and ovum (Table 1). Subsequent western *Isoperla* larval descriptions were published by Bortorff et al. (1990), Szczytko & Stewart (2002), and Baumann & Lee (2009), and none provided a species key. Baumann & Lee (2009) stated that records of *I. fulva* from California were questionable due to its similarity with *Isoperla karuk* Baumann & Lee (*I. roguensis*). Of the three published *I. fulva* locations (Jewett 1960, Szczytko & Stewart 1979), two were revisited and the third, North Fork Feather River,

provided no other location data except for 2,300 feet (701 m) elevation. At the first site, NF Weber Creek, El Dorado County, *Isoperla marmorata* Needham & Claassen was reared and *Isoperla mormona* Banks was collected after multiple visits. The third site, Eagle Creek at Eagleville, Modoc County, may be a possible *I. fulva* location, but immatures that keyed to *Isoperla marmorata* complex were not successfully reared.

A new species key to the mature male larvae occurring in California (including *I. fulva* from

Table 2. *Isoperla* lacinia characters, seta counts from areas A-D and galea seta counts of left and right ventral surfaces (Fig. 1 & Taxonomic Characters). Numbers within parentheses occurred only once. Characters: N = # of lacinia, C/I = Submarginal row Continuous or Interrupted, P/A = Present or Absent, SMR = submarginal row, DS = dorsal seta, DSS = dorsal surface setae, VSS = ventral surface setae, S = galea surface setae, A = galea apical setae.

Species - Male Larvae	Lacinia & Galea Setae Characters and Counts										
	N	SMR	DS	DSS	Submarginal			Marginal	VSS	Galea	
		C/I	P/A	P/A	(A+B)	A	B	C	D	S	A
<i>I. acula</i>	11	I	P	P	4	1-2	2-3	7-9	28-41	42-61	4-5
<i>I. adunca</i>	16	C	P	A	8-11	3-5	4-6	10-13	12-27	12-19	2-3
<i>I. baumanni</i>	17	I	P	P	7-10	5-7	2-3(4)	15-27	38-71	15-33	2-3
<i>I. bifurcata</i>	20	I	P	P	2-4	1-2	1-2	8-11	17-38	37-50	4-6
<i>I. demingi</i>	32	I	P	A	3-4	1	2-3	9-13	11-34	35-48	4-5
<i>I. fulva</i> CO	18	I	P	P	2-3	1	1-2	6-10(11)	64-109	17-30	3-6
<i>I. laucki</i>	10	I	P	P	4	1-2	2-3	(7)8-9	8-13	28-44	4-7
<i>I. marmorata</i>	20	I	P	P	(2)3	1	(1)2	(6)7-10	72-110	19-40	4-5
<i>I. miwok</i>	26	I	P	P	2-3	1	1-2	(5)6-7	7-15	12-26	2-4
<i>I. mormona</i>	25	I	P	P	4	1	3	6-9	7-14	12-17	2-3
<i>I. pinta</i>	20	I	P	P	4	1-2	2-3	4-7	29-50	8-17	4
<i>I. quinquepunctata</i>	20	I	P	P	3(4)	1	2(3)	7-9(11)	48-97	23-27	5
<i>I. roguensis</i>	20	I	P	P	3	1	2	5-8(9)	48-88	19-27	4-6
<i>I. sobria</i>	21	I	P	P	5-6	3-4	2	10-17	21-58	19-23	2
<i>I. sordida</i>	19	I	P	P	3-4	1	2-3	8-11	41-67	20-26	2-5
<i>I. muir</i> OR	17	I	A	P	7-9	2	5-7	9-11	33-58	22-32	5-6
<i>I. tilasqua</i> OR	20	I	P	P	4-7	2-4(5)	(1)2-3	15-20	36-62	11-19	2-3

Table 3. Length and angle measurements of left and right lacinia ventral surfaces (Fig.1). TL = total length, ATL = apical tooth length, STL = subapical tooth length, PL = palm length, PWA = apical palm width, PA = palm angle, PWB = basal palm width.

Species - Male Larvae	Range of Lacinia Character Lengths (µm) & Angle						
	TL(ATL+PL)	ATL	SATL	PL	PWA	PA°	PWB
<i>I. acula</i>	687-786	225-263	124-144	462-523	113-164	52-62	277-311
<i>I. adunca</i>	653-919	188-294	116-180	465-625	142-232	55-70	242-338
<i>I. baumanni</i>	1069-1256	424-506	199-250	645-750	160-227	71-82	363-430
<i>I. bifurcata</i>	666-967	221-348	125-192	445-619	61-145	64-89	280-432
<i>I. demingi</i>	756-1093	256-379	148-217	500-714	117-189	58-79	298-432
<i>I. fulva</i> CO	688-829	229-311	129-168	459-518	67-105	65-87	195-337
<i>I. laucki</i>	839-938	311-355	153-181	528-583	100-119	64-79	324-376
<i>I. marmorata</i>	816-974	254-366	147-187	562-608	98-173	46-73	329-403
<i>I. miwok</i>	622-888	189-308	103-164	433-580	122-185	47-66	262-313
<i>I. mormona</i>	525-666	164-219	93-132	361-447	78-140	51-67	208-259
<i>I. pinta</i>	682-841	245-311	144-171	437-530	74-116	61-78	269-342
<i>I. quinquepunctata</i>	696-828	236-283	134-162	460-545	83-163	55-75	291-353
<i>I. roguensis</i>	682-862	223-313	126-152	459-549	88-175	59-76	284-371
<i>I. sobria</i>	901-1265	323-466	171-244	578-799	126-246	68-84	333-483
<i>I. sordida</i>	856-992	297-347	162-189	559-645	97-153	65-82	344-430
<i>I. muir</i> OR	724-837	235-287	141-159	489-550	128-192	55-69	335-382
<i>I. tilasqua</i> OR	978-1012	376-394	182-197	602-618	161-212	73-79	358-376

Table 4. Length measurements of left and right galea and maxillary palp ventral surfaces (Fig. 1). GL = galea length, PL 1–5 = palp segment length 1–5.

Species - Male Larvae	Range of Galea & Maxillary Palp Segment Lengths (µm)					
	GL	PL 1	PL 2	PL 3	PL 4	PL 5
<i>I. acula</i>	415-556	53-88	137-164	262-290	271-309	229-274
<i>I. adunca</i>	397-518	53-81	130-160	236-267	284-327	207-248
<i>I. baumanni</i>	550-669	69-115	240-299	443-529	463-558	234-350
<i>I. bifurcata</i>	495-625	59-109	101-189	228-339	255-331	216-272
<i>I. denningi</i>	457-716	73-145	152-259	268-403	288-412	248-344
<i>I. fulva</i> CO	349-547	61-114	141-210	259-338	297-347	219-267
<i>I. laucki</i>	542-633	64-88	175-214	342-391	345-408	167-195
<i>I. marmorata</i>	563-743	71-144	179-239	295-368	297-403	220-352
<i>I. miwok</i>	484-663	42-104	93-184	218-352	272-418	271-371
<i>I. mormona</i>	324-479	34-76	92-126	195-246	222-290	201-283
<i>I. pinta</i>	463-605	65-102	126-171	263-333	304-387	273-336
<i>I. quinquepunctata</i>	427-564	55-109	169-220	262-318	263-332	248-296
<i>I. roguensis</i>	468-609	69-123	147-202	254-318	250-361	231-273
<i>I. sobria</i>	519-693	54-111	136-266	354-566	384-617	273-365
<i>I. sordida</i>	531-675	77-142	180-224	316-365	314-384	202-274
<i>I. muir</i> OR	513-601	64-122	151-207	265-302	253-326	175-244
<i>I. tilasqua</i> OR	536-570	69-105	210-221	388-404	447-461	270-295

Colorado and *Isoperla muir* Szczytko & Stewart and *I. tilasqua* from Oregon) is presented utilizing the sclerotized apical structures of the maxilla, lacinia setae characters, maxillary palp setae shape, dorsal femora and tibia setae characters, and pigment patterns. The larval mouth parts of *Isoperla* are classified as Type II for carnivorous food habits (Stewart & Stark 2002). The apical maxilla is composed of three structures: the lacinia, galea and maxillary palp (Fig. 1a & Fig 5.5D in Stewart & Stark, 2002) and the lacinia setae arrangements (marginal, submarginal and ventral surface) offered the most characters for species separation (Stewart & Stark 2002). The lacinia is shaped like a human hand with a central palm like area usually possessing two apically extended teeth on the outer anterior margin and rows or patches of spines on apical, subapical and lateral margins of the palm in ventral view (Stewart & Stark 2002). In one key couplet, fine setae from the dorsal lacinia surface are compared. To observe this character, the compound microscope must be focused downward, through the ventral lacinia surface. It was not possible to separate every species using maxillae characters alone. Those with similar maxilla characters were ultimately separated

by comparing pigment patterns, silky setae characters of the dorsal femora and tibia, and long fine setae of maxillary palp segments 2 and 3.

New terminology used for larval maxilla descriptions are defined in the Taxonomic Characters section and may not apply to immature larvae without developed wingpads. The larval head pigment pattern, maxilla and developing genitalia characters used in all species descriptions are illustrated for *I. baumanni* in Figures 1a-d. Additional measurements not used in descriptions or the species key are provided (Table 3-4). The apical lacinia margin angle (or palm angle) was measured in an attempt to define the lacinia shape.

Taxonomic Characters

Lacinia Structures and Setae Counts (Fig. 1a, Table 1)

- *Apical and Subapical Teeth* (AT & SAT). Long, stout, sharp to blunt anterior apical extensions of the outer lacinia. Very rarely subapical tooth missing or broken.

- *Dorsal Seta* (DS). A single stout seta present on the dorsal lacinia surface, inserted near the base of the subapical tooth inner margin or absent (*I. muir*). Must focus down through subapical tooth to see its point of insertion. Best seen when its apex is unobstructed by subapical tooth, marginal setae or submarginal setae. Not included in setae

counts of Submarginal (A+B) or Submarginal (A) setae.

- *Thin Marginal Seta* (TMS). Present in all species. Probably the axillary seta of other species descriptions (Bottorff et al. 1990, Szczytko & Stewart 2002, 2004). Always a thin single seta inserted on the lacinia margin at the base of the apical tooth inner margin. Sometimes inserted into a short, narrow process raised from the contour of the lacinia margin. Sometimes broken off at various lengths, appearing absent or obstructed from view by overlying submarginal setae or the apical tooth. Not included in setae counts of Submarginal Setae (A+B), or (A).

- *Submarginal Setae* (A+B). Generally a continuous (C) or interrupted (I) row of 2–11 stout, usually longitudinally striated setae inserted below the apical margin and subapical tooth. When continuous (C), the first gap (a space as wide as or wider than bases of adjacent setae) between setae occurs well beyond the subapical tooth inner margin (*I. adunca*). Interrupted rows may begin either as a single seta or as a continuous row of several setae (*Isoperla sobria* complex), but always with a gap occurring before reaching the subapical tooth inner margin. The submarginal row of *I. muir* appears somewhat continuous, but the inter-setae spacing is interpreted here as interrupted. Interrupted submarginal rows are divided into two groups (A+B). Submarginal setae inserted below and between the apical tooth and subapical tooth inner margins are labeled (A) and the submarginal setae row extending beyond the subapical tooth inner margin and ending before reaching the lacinia lateral margin are labeled (B).

- *Submarginal Setae* (A). Row of 1–7 long, stout and usually striated setae. This group of submarginal setae is located closest to apical tooth when row is interrupted by gap. The row extends from the base of apical tooth inner margin and ends before reaching the subapical tooth inner margin.

- *Submarginal Setae* (B). Row of 1–7 long, stout and usually striated setae. This group of submarginal setae is located furthest from apical tooth when row is interrupted by gap. The row extends from just past the subapical tooth inner margin and ends before reaching the lateral lacinia inner margin.

- *Marginal Setae* (C). Row of 4–27 long, stout and usually striated setae. The marginal row begins immediately after the subapical tooth and continues along apical to anterolateral lacinia margins. Sometimes difficult to determine the end of this row because the last few setae decrease in size, becoming close set and blend with ventral surface setae (D) and dorsal surface setae (DSS).

- *Ventral Surface Setae* (D). Fine, occasionally minutely serrated or bifurcate setae inserted near lacinia inner lateral margin. In some species, setae protrude laterally

past inner lacinia margin. Two general arrangements exist: 7–41 scattered setae or 41–110 setae formed into a longitudinal band.

- *Dorsal Surface Setae* (DSS). Fine setae similar to ventral surface setae (D), inserted near the inner lacinia lateral margin on dorsal lacinia surface. Must focus down through ventral surface to view points of insertion. Difficult to distinguish from ventral surface setae when protruding laterally from inner lacinia lateral margin.

Maxilla Length (μm) and Angle Measurements (Fig. 1a, Tables 3-4)

- *Apical Tooth Length* (ATL). Distance between the base and tip of the lacinia apical tooth inner margin.

- *Subapical Tooth Length* (STL). Distance between the median base and tip of the lacinia subapical tooth.

- *Palm Width-Apical* (PWA). Distance between the base of the apical tooth inner margin and the end of the lacinia apical margin.

- *Palm Angle* (PA). Angle of intersect for lacinia apical palm width (PWA) and palm length (PL).

- *Palm Length* (PL). Distance between the base of lacinia outer margin and the base of the apical tooth inner margin.

- *Palm Width-Base* (PWB). Distance between the outer and inner bases of the lacinia.

- *Galea Length* (GL). Polyline distance from base to apex of galea (sum of straight line segments).

- *Palp Length Segments* 1–5 (PL 1–5). Distance between the base and apex of palp segments 1–5 measured along the outer lateral margins. The basal palp segment is PL 1.

Male and Female Larval Sternites (Figs. 1b-c)

The larval species key and descriptions apply to mature male specimens with developed wing pads.

- *Male larvae*. Abdominal segment eight with continuous fringe of stout setae along posterior margin, abdominal segment nine slightly longer than segments eight and ten.

- *Female Larvae*. Abdominal segment eight with median interruption in fringe of stout setae along posterior margin, length of abdominal segment nine similar to segments eight and ten.

Pigment Patterns on Dorsum of Head (Fig. 1d)

- *Anterior Frontoclypeus Area* (a). Unpigmented or light transverse band along the anterior margin. Sometimes connected to light median longitudinal band extending from median ocellus.

- *M Shaped Pattern* (b). Light M shaped transverse line anterior of the median ocellus (Stewart & Stark 2002). The M pattern is present in all the western *Isoperla* species in this study, but sometimes poorly developed or faint. In some species, a variably shaped median longitudinal light

band extends anteriorly from the median ocellus, either connected to the light frontoclypeus or separated by dark pigment (length and width indicated by two crossed arrows in Fig. 1d).

- *Thin Lateral Arms* (c). The lateral arms of the light M shaped pattern. Range from thin to thick, sometimes indistinct or faint.

- *Outer Posterior Ocellus Area* (d). Light areas bordering the outer lateral margins of the posterior ocelli. Light areas small and completely enclosed in dark pigment above the Y arms of the epicranial suture (f), or large and partially enclosed in dark pigment and extending below the Y arms of the epicranial suture (f).

- *Interocellar Area* (e). Variable, from completely dark to entirely light. Usually partially light with some dark pigment within the interocellar triangle, light area either completely within the three ocelli or extending posteriorly, sometimes connected to posterior head capsule by variable shaped light band.

Key to the *Isoperla* of California (including *I. muir* and *I. tilasqua*)

Mature Male Larvae

- 1 Lacinia submarginal setae (Fig. 1a, Fig. 4g) arranged in a close set row, extending past the subapical tooth (SAT) inner margin before the first gap between setae occurs (Fig. 4h) *I. adunca*
- 1' Lacinia submarginal row variable, group (A) setae a close set row, not extending past SAT inner margin (Figs. 5g, 17g & 19g); submarginal row continuous but setae separated by gaps as wide or wider than the width of setae at bases (Fig. 13g); or submarginal row interrupted by large gap between groups A & B (Figs. 3g, 6-12g, 14-16g & 18g) 2
- 2 Lacinia submarginal row (A) with 2-7 closely spaced setae (Figs. 5g-h, 17g-h & 19g-h) omitting thin marginal seta (TMS); pronotum with thick comma shaped dark pigment bands near lateral margins of discs (*I. sobria* complex except *I. miwok*) (Figs. 5b, 17b & 19b) 3
- 2' Lacinia submarginal row (A) with 1 or 2 widely spaced setae (Figs. 3g-h, 6-16g-h & 18g-h) omitting (TMS); pronotum with (*I. miwok*) or without comma shaped pigment bands 5
- 3 Lacinia submarginal row (A) with 5-7 closely spaced setae (Figs. 5g-h); maxillary palp segments 2-3 with curved apically rounded setae (Fig. 5e

- Inset); irregular shaped interocellar light area completely enclosed by dark pigment and known only from Domingo Spring, Plumas County, California *I. baumanni*
- 3' Lacinia submarginal row (A) with 2-5 closely spaced setae (Figs. 17g-h, 19g-h); basal segments 2-3 of maxillary palpi with long, thin, apically rounded or pointed setae; interocellar light area either enclosed or not completely enclosed by dark pigment; variable distribution 4
- 4 Basal segments 2-3 of maxillary palpi with long, thin, apically pointed setae (Fig. 17e Inset); interocellar light area usually an inverted V shape, completely within the three ocelli and enclosed by dark pigment (Fig. 17a); width of median longitudinal light band connecting light M shape to frontoclypeus approximately equal to posteromedian portion of light M shape (Fig. 17a) *I. sobria*
- 4' Basal segments 2-3 of maxillary palpi with long, thin, apically rounded setae (Fig. 19e Inset); interocellar light area not an inverted V shape, usually extending past posterior ocelli to median posterior head capsule light area (Fig. 19a); width of median longitudinal light band connecting light M shape to frontoclypeus approximately half that of posteromedian portion of light M shape (Fig. 19a) *I. tilasqua*
- 5 Lacinia submarginal row (B) with 5-7 setae (Fig. 13g); first marginal seta (C) located under flap-like subapical tooth (SAT) basal inner margin (Fig. 13h), dorsal seta (DS) at base of SAT absent *I. muir*
- 5' Lacinia submarginal row (B) with 1-3 setae; first marginal seta (C) not under flap-like SAT basal inner margin; DS at base of SAT present (Figs. 3g-h, 6-12g-h, 14-16g-h & 18g-h) 6
- 6 Lacinia with first (closest to AT inner margin) submarginal seta (A) inserted closer to middle of subapical tooth base than to apical tooth inner margin (Figs. 11g-h) *I. miwok*
- 6' Lacinia with first submarginal seta (A) inserted closer to base of apical tooth inner margin (Figs. 3g-h, 6-10g-h, 12g-h, 14-16g-h & 18g-h) 7
- 7 Lacinia with 1-2 submarginal setae (A) less than half as stout at base as largest marginal setae (C), longitudinal striations weak or absent (Figs. 14g-h); pronotum with checkerboard pigment pattern

- (Fig. 14b) *I. pinta*
- 7' Lacinia with 1–2 submarginal setae (A) half to nearly as stout at base as largest marginal setae (C), longitudinal striations usually present (Figs. 3g-h, 6-10g-h, 12g-h, 15-16g-h & 18g-h); pronotum without checkerboard pigment pattern (Figs. 3a, 6-10a, 12a, 15-16a & 18a) 8
- 8 Lacinia without dorsal surface setae (DSS), at most the last few marginal setae (C) form a short dorsal row (Fig. 7f - arrow); ventral surface setae (D) concentrated on apical half, few posteriorly *I. denningi*
- 8' Lacinia with dorsal surface setae (DSS) forming a long single row or dense, laterally protruding longitudinal band (Figs. 3f, 6f, 8-12f, 15-16f & 18f); ventral surface setae (D) scattered below marginal and submarginal setae or forming a dense longitudinal band, sometimes concentrated in posterior half 9
- 9 Lacinia with 7–41 ventral surface setae (D) scattered below marginal or submarginal setae (Figs. 3f, 6f, 9f & 12f) 10
- 9' Lacinia with 41–110 ventral surface setae (D) forming dense longitudinal band below marginal or submarginal setae (Figs. 8f, 10f, 15-16f & 18f) 13
- 10 Lacinia with 7–14 ventral surface setae (D) (Figs. 9f, 12f) 11
- 10' Lacinia with 17–41 ventral surface setae (D) (Figs. 3f, 6f) 12
- 11 Fine silky setae sparse on dorsal surfaces of femora and tibia (Fig. 20g); interocellar area completely dark (Fig. 9a); length 9–10 mm *I. laucki*
- 11' Fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20j); interocellar area partially light (Fig. 12a); length 7–9 mm *I. mormona*
- 12 Fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20a); abdomen with median longitudinal thin dark pigment band (Fig. 3d) *I. acula*
- 12' Fine silky setae sparse on dorsal surface of femora, numerous but not continuous on tibia (Fig. 20d); abdomen without median longitudinal dark pigment band (Fig. 6d) *I. bifurcata*
- 13 Pronotal discs mostly dark, each usually with small, light, reticulate markings along median dark pigment margins (*I. marmorata* complex) (Figs. 8a, 10a & 16a) 14
- 13' Pronotal discs patterned, each with variable central light areas generally enclosed by dark pigment (Figs. 15a, 18a) 15
- 14 Dorsal head capsule light M shaped pattern variable, usually not connected to light frontoclypeus area by light longitudinal median band (Figs. 8a, 16a) *I. fulva* & *I. roguensis*
- 14' Dorsal head capsule light M shaped pattern variable, usually connected to light frontoclypeus area by light longitudinal median band (Fig. 10a) *I. marmorata*
- 15 Fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20m); faint M shaped light pattern on dorsum of head completely enclosed by dark pigment (Fig. 15a); pronotum pattern variable with small to large irregular shaped window-like light areas on each disc (small in Fig. 15b), specimens with large window like light areas usually partially open along inner margins *I. quinquepunctata*
- 15' Fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20p); M shaped light pattern on dorsum of head connected to unpigmented frontoclypeus by median light band (Fig. 18a); pronotum pattern less variable, with large irregular shaped window-like light areas on each disc (Fig. 18b), window-like light areas enclosed by dark pigment along inner margins *I. sordida*
- Isoperla acula* Jewett**
(Figs. 2a, 3a-h, 20a)
- Isoperla acula* Jewett 1962, 38:18.
Isoperla acula: Szczytko & Stewart 1979, 32:77.
Isoperla acula: Bottorff et al. 1990, 92:291-294. Larva (reared).
- Material examined.** TYPE: *I. acula*, Holotype ♂, CA: Fresno Co., 7 mi NE Academy, elev. 800 feet, Dry Cr., 19/IV/1955, D.L. Abell (CAS #8591). **Additional Specimens.** CALIFORNIA: **Amador Co.**, Big Indian Creek, 2 km S NF Cosumnes R., Hwy 49, 25/IV/1986, R.L. Bottorff, Larvae (NMNH); Big Indian Creek, Hwy 49, 2.9 mi N Plymouth, unnamed rd. xing, 25/IV/2009, J. Sandberg, Larvae; Little Indian Creek, 3



Figs. 2a-q. *Isoperla* lacinia habitus, 40x, Bar = 500µm. 2a. *I. acula*; 2b. *I. adunca*; 2c. *I. baumanni*; 2d. *I. bifurcata*; 2e. *I. denningi*; 2f. *I. fulva*; 2g. *I. laucki*; 2h. *I. marmorata*; 2i. *I. miwok*; 2j. *I. mormona*; 2k. *I. muir*; 2l. *I. pinta*; 2m. *I. quinquepunctata*; 2n. *I. roguensis*; 2o. *I. sobria*; 2p. *I. sordida*; 2q. *I. tilasqua*.

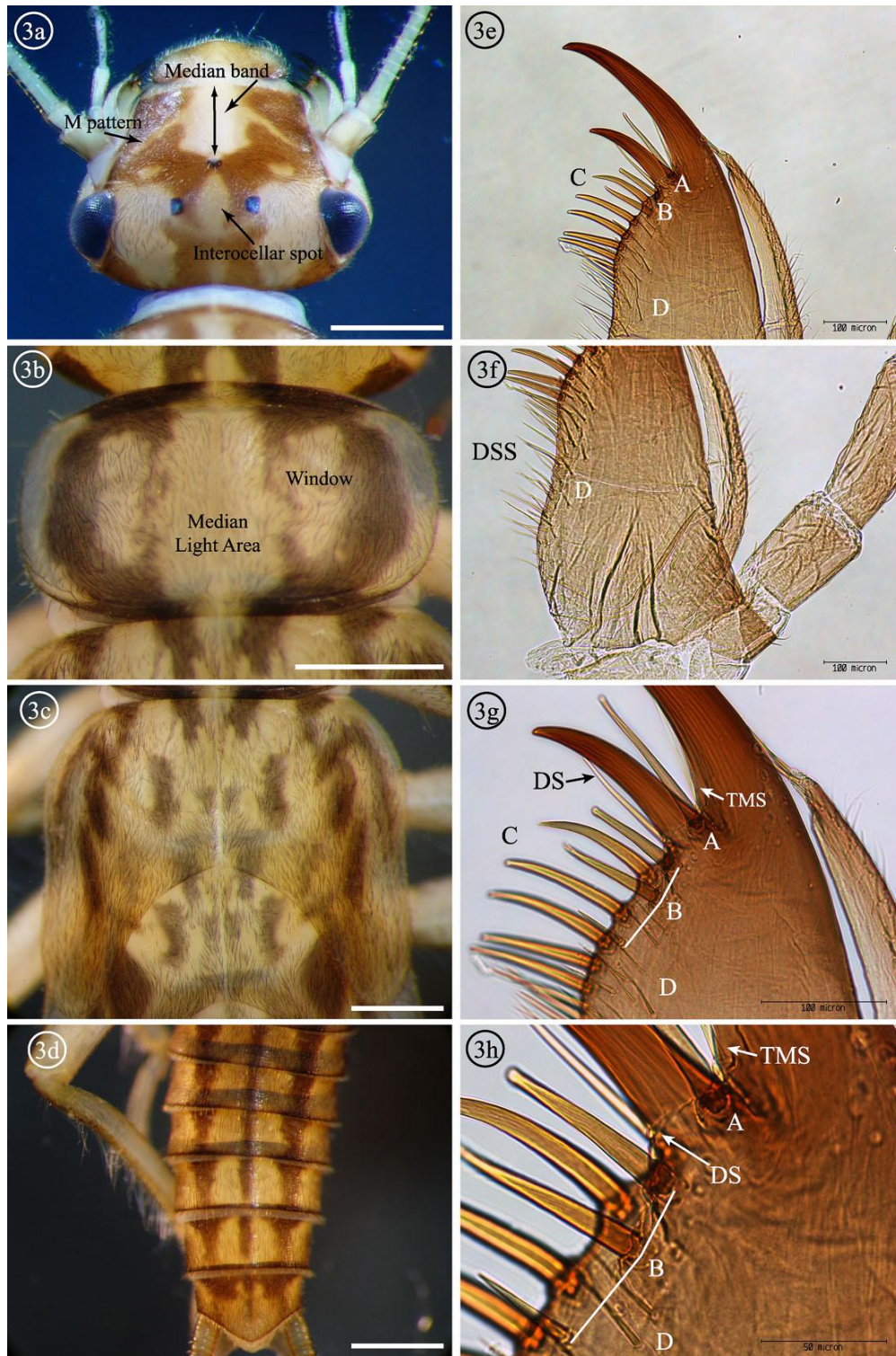
km W Plymouth, 25/IV/1986, R.L. Bottorff, Exuviae (NMNH); Little Indian Creek, 3 km W Plymouth, 12/V/1987, R.L. Bottorff, ♂♀ reared, Larvae (CAS); Little Indian Creek, 3 km W Plymouth, 12/V/1987, R.L. Bottorff, ♂♀ reared (NMNH). **Butte Co.**, ?, 9 mi N Oroville, 24/IV/1955, S.W. Hitchcock, ♂, Larvae (NMNH); **El Dorado Co.**, Cooper Canyon Creek, Rattlesnake Bar Rd. xing, 2.25 mi SE Hwy 49, 30/III/2009, J. Sandberg, Larvae; Deadman Creek, Church Mine Rd. xing, 2.45 mi SE El Dorado, 30/III/2009, J. Sandberg, Larvae; J. Sandberg, D. Pickard, 04/IV/2009, Larvae; 05/IV/2009, Larvae; 25/IV/2009, Larvae (reared); 10/V/2009, Larvae (reared); 16/V/2009, Larvae (reared); 23/V/2009, ♂♀, Larvae (reared); Martinez Creek, Martinez Cr. Rd., 3.5 mi SE El Dorado, 04/IV/2009, J. Sandberg, D. Pickard, Larvae; NF Cosumnes River, Hwy 49 cattle coral, 1.7 mi S Nashville, below confluence w/MF Cosumnes R., 28/III/2009, J. Sandberg, Larvae; Tributary of NF Cosumnes River, ~2 km W Martinez Cr., S El Dorado, 12/V/1987, R.L. Bottorff, 12/V/1987, ♂♀, Larvae (CAS); Tributary of NF Cosumnes River, Union Mine Rd., 3.4 mi (5.5 km) N Nashville at McNulty Mine Rd. xing, 25/IV/2009, J. Sandberg, Larvae (reared).

Male larva. Body length of mature larva 10–11 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus connected to light frontoclypeus area by median longitudinal light band, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area partially light and generally diamond shaped, completely enclosed by dark pigment, light area extending past posterior ocelli, reaching dark pigment below the arms of the epicranial suture; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 3a). **Lacinia** bidentate, total length 687–786 μm (Fig. 2a, 3e-h, Tables 2-4); submarginal row (A+B) with 4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 3h); 1–2 submarginal setae (A), the first inserted at base of apical tooth (AT) inner margin, the second when present, located between AT and SAT inner margins,

plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT or broken, and 1 dorsal seta (DS) located below SAT inner margin sometimes obstructed by SAT (Figs. 3g-h); 2–3 submarginal setae (B) located past SAT inner margin (Figs 3g-h); 7–9 marginal setae (C) initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 3e); 28–41 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length (Fig. 3f); dorsal surface setae (DSS) continue from last marginal seta (C) as a single, laterally protruding, submarginal row along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 3f). **Galea** with 42–61 setae in thick ventral band, apex with 4–5 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area bordered (at least partially) by thin, irregular dark bands; discs each with partially to totally enclosed light areas or “windows” and fine dark clothing setae, lateral margins with broad light bands (Fig. 3b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 3c). **Legs** with numerous fine dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20a); tibia with faint transverse bands near proximal end. **Abdominal terga** with three distinct longitudinal dark stripes; wide light median longitudinal band bisected with thin dark median longitudinal stripe; lateral pair of dark longitudinal stripes about twice as wide as median dark stripe, not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 3d).

Distribution. California: Sierra Nevada foothills.

Diagnosis. Among the male larvae with 2–4 submarginal row (A+B) setae (Table 2), *I. acula* is most similar to *I. bifurcata* (Figs. 3a-h, 6a-h). Characters that distinguish this species from *I. bifurcata* include fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20a), and abdomen with median longitudinal



Figs. 3a-h. *Isoperla acula* nymph and ventral maxilla, Deadman Creek, El Dorado County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 3e-f 100x, 3g 200x, and 3h 400x.

thin dark pigment band (Fig. 3d).

Remarks. *Isoperla acula* co-occurred with *I. adunca*, *Isoperla miwok* Bottorff & Szczytko, and *I. marmorata* in mostly non-perennial and one perennial central Sierra Nevada foothill streams. Emergence occurred in April–May (lasting to early June in wetter years) and life history studies are needed to determine how *I. acula*, *I. adunca* and *I. miwok* cope with shortened surface flow periods. It is suspected that larvae move to hyporheic zones when stream flow ceases in late summer.

Isoperla adunca Jewett
(Figs. 2b, 4a-h, 20b)

Isoperla adunca Jewett 1962, 38:19.

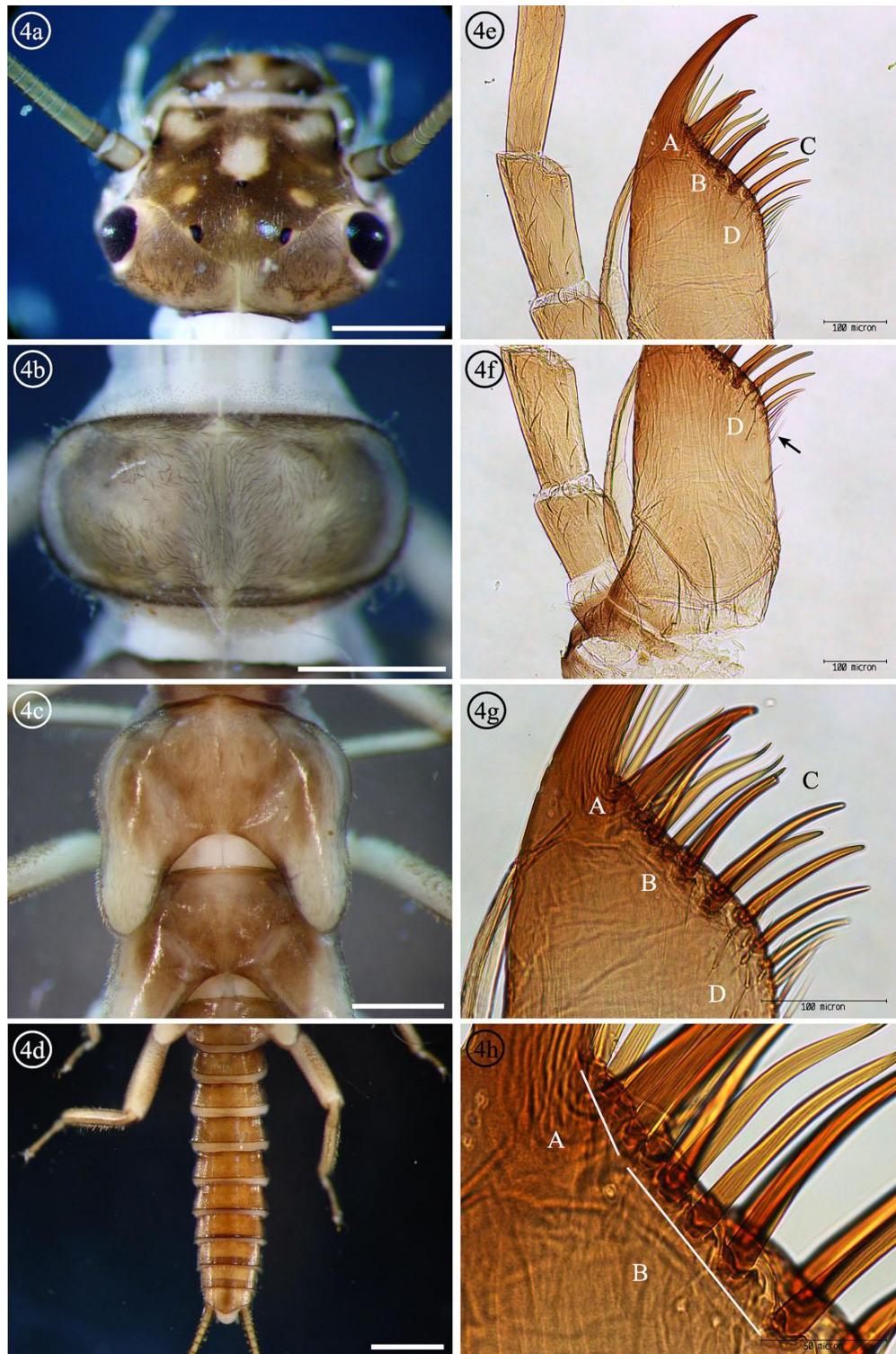
Isoperla adunca: Szczytko & Stewart 1979, 32:80.

Isoperla adunca: Bottorff et al. 1990, 92:294-299. Larva (reared).

Material examined. TYPES: *I. adunca*, Holotype ♂, CA: **Santa Clara Co.**, 5 mi E Mt. Hamilton, Isabel Creek?, 31/V/1949 (CAS #8592). Paratype ♂, CA: **Tuolumne Co.**, Keystone, 25/IV/1951, J.W. MacSwain (CAS). Paratype ♂ and ♀, same as Holotype, (CAS). **Additional Specimens.** CALIFORNIA: **Alameda Co.**, Indian Creek, 1.8 mi (2.9 km) upstream of San Antonio Reservoir, 25/V/2010, Larva (ABL); **Amador Co.**, Big Indian Creek, N Plymouth, 25/IV/1986, R.L. Bottorff, Larvae (NMNH); Big Indian Creek, N Plymouth, 9/V/1986, R.L. Bottorff, ♀, Larvae (NMNH); Big Indian Creek, N Plymouth, 30/V/1986, R.L. Bottorff, Larvae (NMNH); Big Indian Creek, Hwy 49, 2.9 mi (4.7 km) N Plymouth, 4/IV/2009, J. Sandberg, D. Pickard, Larvae; Big Indian Creek, Hwy 49, 2.9 mi (4.7 km) N Plymouth, 25/IV/2009, J. Sandberg, Larvae (reared); Little Indian Creek, 3 km W Plymouth, 25/IV/1986, R.L. Bottorff, ♂ (everted), Larvae (NMNH); Little Indian Creek, 3 km W Plymouth, 12/V/1987, R.L. Bottorff, ♂♀, Larvae (NMNH); Little Indian Creek, Old Sacramento Rd xing, 1.5 mi (2.4 km) W Plymouth, 4/IV/2009, J. Sandberg, D. Pickard, Larvae; **Butte Co.**, Clear Creek, at Hwy 149, between Hwys 99 & 70, T1-3, 4/IV/2004, Larvae (ABL); Dry Creek, at Hwy 149, between Hwys 99 & 70, T1-2, 4/IV/2004, Larvae (ABL); Campbell Creek & tributary, North Table Mountain Wildlife Area, Cherokee Rd, 5 mi (8 km) S Cherokee,

3/III/2007, J. Sandberg, Larvae (reared); 7/IV/2007, Larvae (reared); 13/IV/2007, ♂♀, Larvae (reared); 18/IV/2007, Larvae; 23/II/2008, Larvae; 24/III/2008, Larvae; 30/III/2008, Larvae; 30/IV/2008, Larvae; 2/V/2010, J. Sandberg, A. Richards, Larvae (reared); **Contra Costa Co.**, Mitchell Creek, 0.5 mi (0.8 km) below Uncle Sam Canyon, R1, 22/IV/2009, Larvae (ABL); Mitchell Creek, 250m upstream of bridge at Mt. Diablo State Park entrance, 24/V/2010, Larva (ABL); **El Dorado Co.**, SF Cosumnes River, Site 22, R2, 28/V/1995, Larvae (ABL); Deadman Creek, Church Mine Rd xing, 2.4 mi (3.9 km) SE El Dorado, 10/V/2009, 16/V/2009, 23/V/2009, J. Sandberg, ♂♀, Larvae (reared); Greenwood Creek, Greenwood Creek Park, Hwy 49, 4 mi (6 km) E Pilot Hill, 10/V/2009, J. Sandberg, Larvae; **Fresno Co.**, Mill Creek, Rt 180, E Fresno, 1800 feet, 7/VI/1963, C.P. Alexander, ♂♀ (NMNH); **Sacramento Co.**, Cosumnes River, at Michigan Bar, 6/VII/1982, R.L. Bottorff, Larvae (ABL); **San Diego Co.**, Nobel Canyon Creek, 0.8 mi (1.3 km) above Pine Valley Cr., R1, 28/IV/2009, Larvae (ABL); San Diego River, Headwaters above Hwy 79, 04/V/2010, Larvae (ABL); San Luis Rey River WF, 1 mi (1.6 km) N Mendenhall Valley, R1, 28/IV/2009, Larvae (ABL); **Santa Clara Co.**, Coyote Creek, Gilroy Hot Springs Road, 1.4 mi N Gilroy Hot Springs, 26/VI/2010, J. York, ♂♀; **Ventura Co.**, Sespe Creek, Hwy 33, approximately 19.5 mi (31.4 km) NW of Wheeler Springs, 07/VI/2010, Larvae (ABL).

Male larva. Body length of mature larva 9–10 mm. **Dorsum of head** mostly dark with fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus present but poorly defined, not connected to light frontoclypeus area, median longitudinal pigment band short, nearly square, lateral thin arms indistinct, directed posterolaterally and extending to antennal bases; posterior ocelli with completely enclosed small light areas along outer lateral margins; interocellar area mostly dark, usually a small unpigmented central area completely enclosed by dark pigment; occiput with irregular spinulae band extending from below eye to near median epicranial suture, partially to completely enclosed by indistinct dark pigment (Fig. 4a). **Lacinia** bidentate, total length 653–919 µm (Fig. 2b, 4e-h, Tables 2-4); submarginal row (A+B) with 8–11 setae, groups A-B continuous



Figs. 4a-h. *Isoperla adunca* nymph and ventral maxilla, Campbell Creek, Butte County, CA. Submarginal setae groups A and B, Marginal setae C, and Ventral surface setae D. White bars = 1 mm, 4e-f 100x, 4g 200x, and 4h 400x.

below subapical tooth (SAT) inner margin (Figs. 4g-h); 3–5 submarginal (A) setae and 4–6 (B) setae in a row without gap between setae until past SAT inner margin, row extending from base of apical tooth (AT) to nearly lacinia lateral margin, the last 3–4 setae becoming widely spaced, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by apical tooth, first submarginal seta or broken, and 1 dorsal seta (DS) located below subapical tooth inner margin, partially obstructed from view by first few submarginal setae (Fig. 4h); 10–13 marginal setae (C) initially long-stout and widely spaced, last few shorter, variably spaced and occasionally borne from dorsal surface (Figs. 4e, 4g); 12–27 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, occasionally a few setae below submarginal row striated (Fig. 4f); dorsal surface setae (DSS) usually absent, sometimes last few marginal setae (C) form a short dorsal row (Fig. 4f – arrow); 15–20 minute scale-like spinulae rarely present on and along ventral inner-lateral margin in basal half. **Galea** with 12–19 setae in sparse ventral row, apex with 2–3 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with indistinct and variable pigment pattern, median light area absent and fine dark clothing setae; discs occasionally with slightly darker comma shaped areas near lateral margins, lateral margins with broad light bands (Fig. 4b). **Meso and metanotum** with indistinct pigment pattern and fine dark clothing setae (Fig. 4c). **Legs** with numerous fine light brown clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20b); tibia with faint transverse bands near proximal end. **Abdominal terga** without distinct longitudinal dark stripes; numerous fine light clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 4d).

Distribution. California: Sierra Nevada foothills.

Diagnosis. The lacinia of male *I. adunca* larvae are distinctive in that the entire submarginal row (A+B) is continuous from the base of the apical tooth continuing to almost the inner lacinia margin (Figs.

4g-h). Larvae lack distinct pigment patterns, especially longitudinal abdominal stripes. The lacinia of immature larvae are also distinct and resemble mature larvae, except that submarginal row (A+B) setae are more widely spaced.

Remarks. *Isoperla adunca* inhabits mostly non-perennial and a few perennial foothill streams of the central Sierra Nevada range. It co-occurred with the following species: *I. acula*, *I. marmorata*, *I. miwok*, and *Isoperla mormona* Banks and emergence occurred in April–June.

Isoperla baumannii Szczytko & Stewart
NEW LARVA DESCRIPTION
(Figs. 1a-d, 2c, 5a-h, 20c)

Isoperla baumannii Szczytko & Stewart 1984, 77:258-260.

♂, ♀, Ovum unknown.

Isoperla baumannii Szczytko & Stewart 2002, 128:2-3.

Larva (not reared) = *I. bifurcata*.

Material examined. TYPES: *I. baumannii*, Holotype ♂, Allotype ♀, CA: **Plumas Co.**, Domingo Springs Campground, 6 mi (9.7 km) NW Chester, Domingo Spring, 25/VI/1980, R. Baumann, J. Stanger (NMNH #104070). **Additional Specimens.** CALIFORNIA: **Plumas Co.**, Domingo Spring, Domingo Springs Campground, 8.5 mi (13.7 km) NW Chester on Old Red Bluff Rd., 20/I/2007, J. Sandberg, Larvae; 04/II/2007, Larvae; 24/III/2007, Larvae; 09/VI/2007, J. Sandberg, A. Richards, Larvae (reared); 13/VI/2007, J. Sandberg, ♂♀, Larvae (reared); 17/VI/2007, ♂♀, Larvae (reared); 07/VII/2007, ♂♀ Larvae; 03/XI/2007, Larvae; 02/V/2008, J. Sandberg, D. Pickard, Larvae; 17/V/2008, J. Sandberg, Larvae; 13/VI/2008, Larvae (reared); 20/VI/2008, ♂♀ Larvae (reared); 22/VI/2008, ♂♀, Larvae; 05/VI/2010, Larvae (reared); 03/VII/2010, ♂♀.

Male larva. **Body** length of mature larva 9–10 mm.

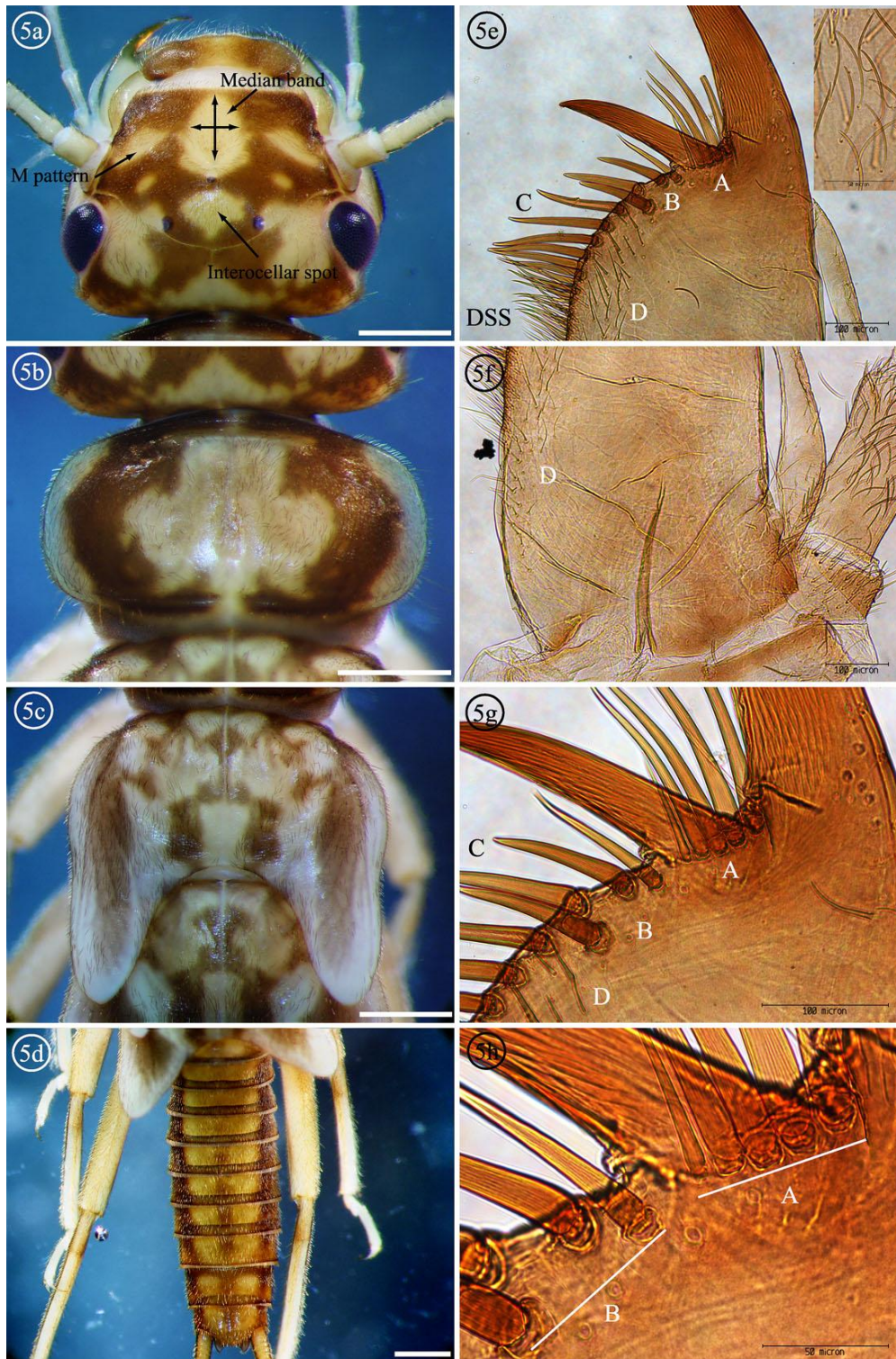
Dorsum of head with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus usually connected to light frontoclypeus area by an apically narrowed median longitudinal light band, its width at mid length approximately equal to the width at base, lateral arms with irregular margins usually disconnected from median light band, directed posterolaterally,

and extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area partially light, completely enclosed by dark pigment, light area extending past posterior ocelli, not reaching dark pigment below the arms of the epicranial suture, light area generally oval shaped with acutely constricted base; occiput with irregular spinulae band extending from below eye to near median epicranial suture, completely enclosed by dark pigment (Figs. 1d, 5a). **Lacinia** bidentate, total length 1069–1256 μm (Figs. 1, 2c, 5e-h, Tables 2-4); submarginal row (A+B) with 7–10 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 5g); 5–7 submarginal setae (A) in a close set row beginning at base of apical tooth (AT), ending before reaching SAT inner margin, row usually single, rarely 2 setae thick, plus 1 thin marginal setae (TMS) adjacent to AT inner margin, sometimes obstructed from view by the AT, submarginal setae (A), or broken, and 1 dorsal seta (DS) located below SAT inner margin, sometimes obstructed from view by SAT, submarginal setae (B), or broken (Fig. 5h); 2–4 submarginal setae (B) located past SAT inner margin (Figs. 5g-h); 15–27 marginal setae (C) initially long-stout and widely spaced, usually several setae near end of row arranged in pairs protruding at dorsal and ventral angles, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 5e); 38–71 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, occasionally a few setae below submarginal row striated (Fig. 5f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band, concentrated at junction with marginal setae (C), ending at approximately $\frac{1}{2}$ or a little more the lacinia length (Fig. 5e). **Galea** with 15–33 setae in sparse ventral row, apex with 2–3 setae. **Maxillary Palp** segments 2–3 with curved apically rounded setae (Fig. 5e Inset). **Pronotum** with broad median light area bordered by thick dark comma shaped bands typical of the *I. sobria* complex; discs each with thick black clothing setae, those along median margins usually enclosed by indistinct light brown pigment, lateral margins with broad light bands (Fig. 5b). **Meso and metanotum** with contrasting pigment pattern and

fine dark clothing setae (Fig. 5c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20c); tibia with faint transverse bands near proximal end. **Abdominal terga** with three longitudinal dark stripes; wide light median longitudinal band bisected with thin light brown median longitudinal stripe present on distal segments; lateral pair of dark longitudinal stripes about twice as wide as median dark stripe, extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 5d).

Distribution. Northern California, known only from one Sierra Nevada high elevation spring.

Diagnosis. The 5–7 submarginal (A) setae of *I. baumanni* male larvae (Figs. 5g-h) are most similar to *Isoperla sobria* (Hagen) and *I. tilasqua* but differs from *I. miwok* with only one submarginal (A) seta (Fig. 11g). The setae counts alone were not sufficient to separate the three species with multiple close set submarginal (A) setae; *I. sobria* with 3–4 submarginal (A) setae (Figs. 17e, g-h) and 2-5 submarginal (A) setae for *I. tilasqua* (Figs. 19e, g-h). It is suspected that increased variation will be observed as more populations are studied. The basal segments 2–3 of the maxillary palpi have long, thin, apically rounded setae (Fig. 5e Inset) which are shared by *I. tilasqua* (Fig. 19e Inset); *I. sobria* has long thin, apically pointed setae (Fig. 17e Inset). The variably shaped and large *I. baumanni* interocellar light area is completely enclosed by dark pigment (Fig. 5a), similar to *I. sobria* (Fig. 17a), but the latter is usually an inverted V shape (or sometimes a very small light spot). The interocellar light area of *I. tilasqua* (Meacham Creek, Oregon population) is not completely enclosed by dark pigment, and continues past the posterolateral ocelli to the median base of the dorsal head capsule (Fig. 19a). The light M shaped dorsal head pattern of *I. tilasqua* is a continuous line, but is interrupted in *I. baumanni* and *I. sobria*. A median longitudinal light band is present in all three species, but this line is approximately half as wide as the median base of the light M pattern in *I.*



Figs. 5a-h. NEW DESCRIPTION of *Isoperla baumannii* nymph and ventral maxilla, Domingo Spring, Plumas County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, and Dorsal surface setae DSS. Fig. 5e Inset: Maxillary palp segment 2 with apically rounded long thin setae, 400x. White bars = 1 mm, 5e-f 100x, 5g 200x, and 5h 400x.

tilasqua (Fig. 19a).

Remarks. *Isoperla baumanni* may be restricted to Domingo Spring, Plumas County, a high volume and nearly stenothermic spring and emergence occurred in June–July. It was absent in nearby smaller Mosquito Spring containing both *I. bifurcata* and *I. sobria*, and an unnamed spring tributary to Gurnsey Creek with only *I. bifurcata* present. Recent collecting and rearing at Domingo Springs from 2006–2010 confirm three sympatric species: *I. baumanni*, *I. bifurcata*, and *I. marmorata* (three collected adults only). *Isoperla bifurcata* larvae were distributed throughout the spring and collected from all available submerged substrates (aquatic moss, aquatic plants, wood and rock). *Isoperla baumanni* larvae were primarily collected from submerged aquatic liverworts located in a small area along the southeastern bank, below the footbridge and above the cattle fence.

Everted *I. baumanni* males (reared & collected) did not compare well with the original description and appears to be the result of using two methods for everting the aedeagus. The aedeagus illustrated by Szczytko & Stewart (1984 – Fig. 53) was cleared and then hyper everted and this method may not be directly comparable to males that were everted live. Attempts to produce a similar eversion as illustrated in Szczytko & Stewart (1984) resulted in bursting the aedeagus membrane. In the current study, 31 reared and fully everted males lacked the projected, conical, anterodorsal striated, bladelike tip. Instead, a small depression was visible in this area and when the freshly everted aedeagus was fixed in near boiling water, seminal fluid streamed from the depression. The absence of long, paired membranous lobes was also observed in *I. fulva*, *I. miwok*, and *I. roguensis*, emphasizing the difference between live everted specimens of the current study and hyper everted preserved specimens illustrated in previous studies. Perhaps the striated bladelike tip of the *I. baumanni* aedeagus as illustrated in Szczytko & Stewart (1984) is an internal valve, which controls the release of sperm during copulation.

Two mature male larvae from Long Canyon Creek, El Dorado County, California were prepared for maxillae examination and tentatively identified as *I. baumanni*. The partly mature larvae with developing wing pads were collected on April 27th,

2007, by Austin Brady Richards near Bendorf Spring. Both the males and females in the sample possessed an inverted V shaped light mark within the intercellular area, similar to *I. sobria*. One unsuccessful return trip by the author was conducted in early July, 2011, to attempt rearing and adult collection.

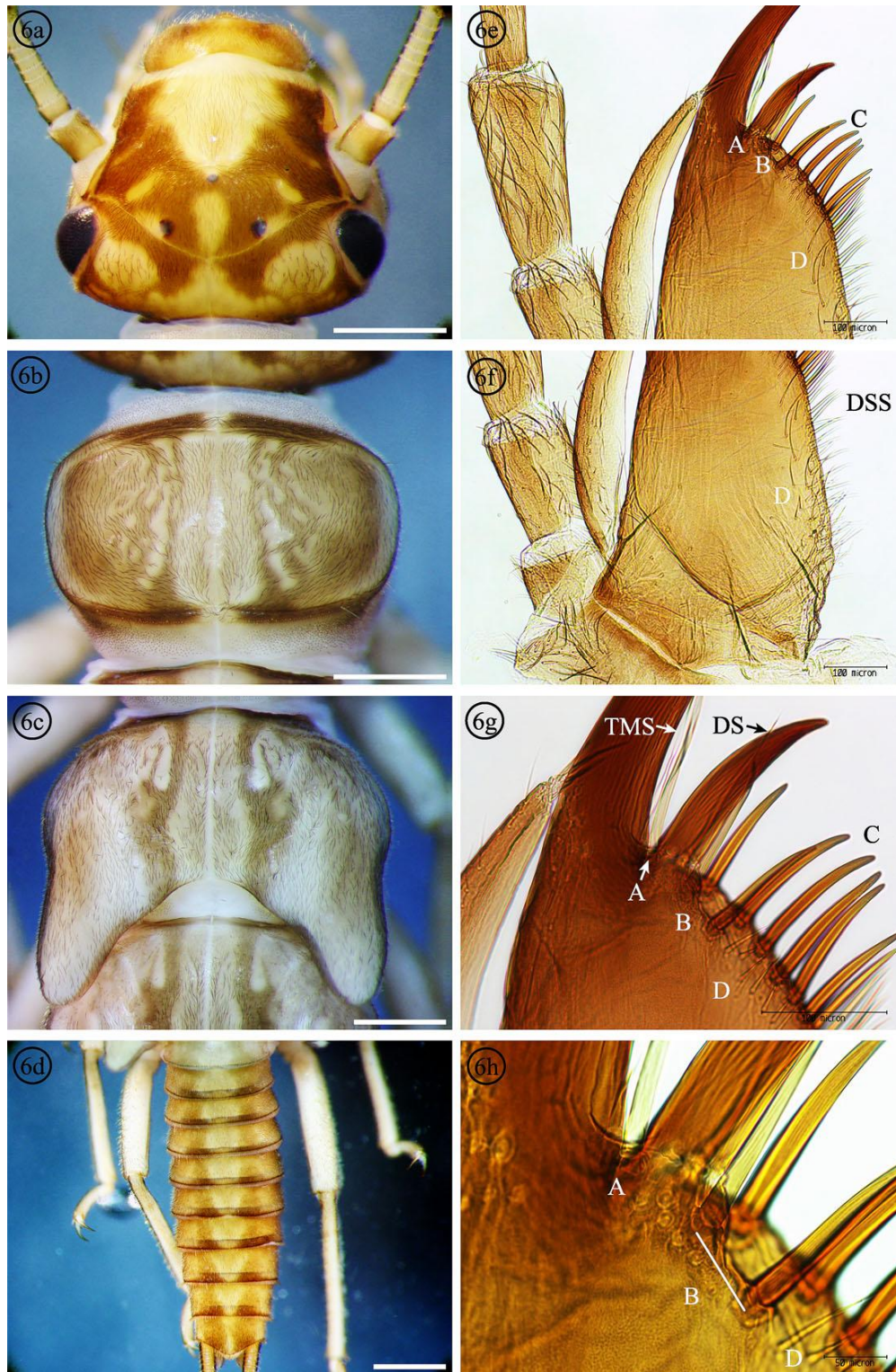
Isoperla bifurcata Szczytko & Stewart
(Figs. 2d, 6a-h, 20d)

Isoperla bifurcata Szczytko & Stewart 1979, 32:80-84, 86.
Isoperla bifurcata: Bottorff et al. 1990, 92:299-302. Larva (reared).
Isoperla baumanni Szczytko & Stewart 2002, 128:2-3. Larva (not reared) = *I. bifurcata*.

Material examined. TYPES: *I. bifurcata*, Holotype ♂, OR: **Union Co.**, ~6 mi (9.7 km) E Medical Springs, DFTM Proj., Lick Creek, 23/VII/1975, D. Dunster (NMNH #76343); Allotype ♀, same location and collector, 30/VI/1976 (NMNH); Paratype ♂♀, same location and collector as Holotype, 23/VII/1975 (NMNH). **Additional Specimens.** CALIFORNIA: **Butte Co.**, Butte Creek, Butte Meadows Campground, Humbug Rd., Butte Meadows, 30/III/2007, J. Sandberg, Larvae; Butte Creek, Cherry Hill Campground, Humbug Rd., 9 mi (14.5 km) NE Lomo (Hwy 32), 18/II/2007, J. Sandberg, D. Pickard, Larvae. **El Dorado Co.**, NF Cosumnes River, Headwaters below Singleton Springs, E Grizzly Flat, 22/VI/1987, R. Bottorff, Larvae (NMNH); NF Cosumnes River, Headwaters below Singleton Springs, E Grizzly Flat, 22/VI/1987, R. Bottorff, Larvae (CAS). **Fresno Co.**, Huntington Lake, 07/VII/1919, F. Blasdel, ♂ (NMNH). **Plumas Co.**, Domingo Spring, Domingo Springs Campground, 8.5 mi (13.7 km) NW Chester on Old Red Bluff Rd., 12/VIII/2006, J. Sandberg, J. Slusark, Larvae; 01/X/2006, J. Sandberg, ♂♀, Larvae (mature and early instar); 10/XII/2006, Larvae; 20/I/2007, Larvae; 04/II/2007, Larvae; 24/III/2007, Larvae; 22/IV/2007, Larvae (reared); 06/V/2007, J. Sandberg, D. Pickard, Larvae; 19/V/2007, J. Sandberg, S. Hassur, Larvae (reared); 28/V/2007, J. Sandberg, D. Pickard, Larvae (reared); 09/VI/2007, J. Sandberg, A. Richards, ♂, Larvae (reared), Exuviae; 13/VI/2007, J. Sandberg, ♂♀, Larvae (reared); 17/VI/2007, ♂♀; 07/VII/2007, ♂♀; 01/VIII/2007, ♀, Larvae; 16/IX/2007, ♂♀, Larvae;

21/IX/2007, ♂♀, Larvae; 30/IX/2007, ♀; 03/XI/2007, ♂♀, Larvae; 20/V/2008, J. Sandberg, D. Pickard, Larvae; 17/V/2008, Larvae; 13/VI/2008, ♂♀; 20&22/VI/2008, ♂♀; 06/IX/2008, ♂-♀; 05/VI/2010, Larvae (reared); 03/VII/2010, ♂; Mosquito Creek (East Branch), 0.6 mi (1 km) E of Domingo Springs, 7.9 mi (12.7 km) W of Chester, 04/II/2007, J. Sandberg, Larvae; 01/IV/2007, Larvae; Mosquito Creek (West Branch), 0.4 mi (0.6 km) E of Domingo Springs, 8.1 mi (13.0 km) W of Chester, 04/II/2007, J. Sandberg, Larvae; 24/III/2007, Larvae; 22/IV/2007, J. Sandberg, D. Pickard, Larvae (reared); 19/V/2007, J. Sandberg, S. Hassur, Larvae (reared); 28/V/2007, J. Sandberg, D. Pickard, ♂, Larvae (reared); 13/VI/2007, J. Sandberg, ♂♀, Larvae (reared); 01/VIII/2007, Larvae; 11/VIII/2007, Larvae; 16/IX/2007, Larvae; 21/IX/2007, Larvae; 03/XI/2007, Larvae; 17/V/2008, Larvae; 13/VI/2008, Larvae (reared); 20/VI/2008, ♂♀, Larvae (reared); 05/VI/2010, Larvae; 03/VII/2010, ♂♀. **Siskiyou Co.**, Big Springs Creek, Big Springs Park, Nixon Rd., Mt. Shasta, 13/V/2007, J. Sandberg, D. Pickard, Larvae. **Tehama Co.**, Spring Trib of Gurnsey Creek, Gurnsey Creek Campground, Hwy 36, 2.3 mi (3.7 km) N Hwy 32 Intersec., 26/IV/2010, R. Baumann, B. Kondratieff, A. Richards, J. Sandberg, J. Slusark, Larvae (reared). **Trinity Co.**, ?, Carrville, ?/VI/1913, E.C. VanDyke, ♂♀ (CAS). **Tulare Co.**, Marble Fork Kaweah River, Sequoia Nat. Pk., 24/VII/1907, J. Bradley, ♂ (NMNH). OREGON: **Union Co.**, Lick Creek, about 6 mi (9.6 km) E Medical Springs, 30/VI/1976, D. Dunster, ♀ (NMNH). **Male larva.** Body length of mature larva 9–11 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus connected to light frontoclypeus area by broad median longitudinal light band, lateral thin arms directed posterolaterally, and extending to antennal bases; posterior ocelli with completely enclosed small light areas along outer lateral margins; interocellar area partially light and variable, from completely enclosed by dark pigment to open posteriorly and connected to light area below occipital spinulae band; occiput with irregular spinulae band extending from below eye to near median epicranial suture, enclosed by dark and light brown pigment (Fig. 6a). **Lacinia** bidentate, total length 666–967 μm (Figs. 2d, 6e-h, Tables 2-4);

submarginal row (A+B) with 2–4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Figs. 6g-h); 1–2 submarginal setae (A) the first inserted at base of apical tooth (AT) inner margin, the second when present, located between SAT and AT inner margins, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal setae (A), or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 6g-h); 1–2 submarginal setae (B) located past SAT inner margin (Figs. 6g-h); 8–11 marginal setae (C) initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 6e); 17–38 ventral surface setae (D) scattered below submarginal and marginal setae ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length (Fig. 6f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface seta (Fig. 6f). **Galea** with 37–50 setae in thick ventral band, apex with 4–6 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** generally light brown, median light area bordered laterally by dark brown pigment and light rugosities; discs each with thin, dark brown comma shaped areas near lateral margins and fine dark clothing setae, lateral margins with broad light bands (Fig. 6b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 6c). **Legs** with numerous fine dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous but not continuous on tibia (Fig. 20d); tibia with very faint transverse bands near proximal end. **Abdominal terga** with two distinct longitudinal dark stripes; wide light median longitudinal band occasionally appears bisected by muscle attachment scars; lateral pair of dark longitudinal stripes usually not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 6d). **Distribution.** Northern California (Sierra Nevada high elevation springs and creeks), Idaho, and Oregon.



Figs. 6a-h. *Isoperla bifurcata* nymph and ventral maxilla, Mosquito Spring, Plumas County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 6e-f 100x, 6g 200x, and 6h 400x.

Diagnosis. Male larvae of *I. bifurcata* are most similar to *I. acula* and can be separated by having fine silky setae sparse on dorsal surface of femora, numerous but not continuous on tibia (Fig. 20d), and abdomen without a distinct median dark stripe (Fig. 6d).

Remarks. This species was the lone *Isoperla* species or occurred with either *I. baumanni* or *I. sobria* in small to large, mid-elevation spring creeks in the Sierra Nevada range of California. Emergence was extended at Domingo and Mosquito Springs, Plumas County, and occurred in May–October. An extended summer–fall emergence was also observed for *I. laucki*.

Isoperla denningi Jewett
(Figs. 2e, 7a-h, 20e)

Isoperla denningi Jewett 1955, 13:150.

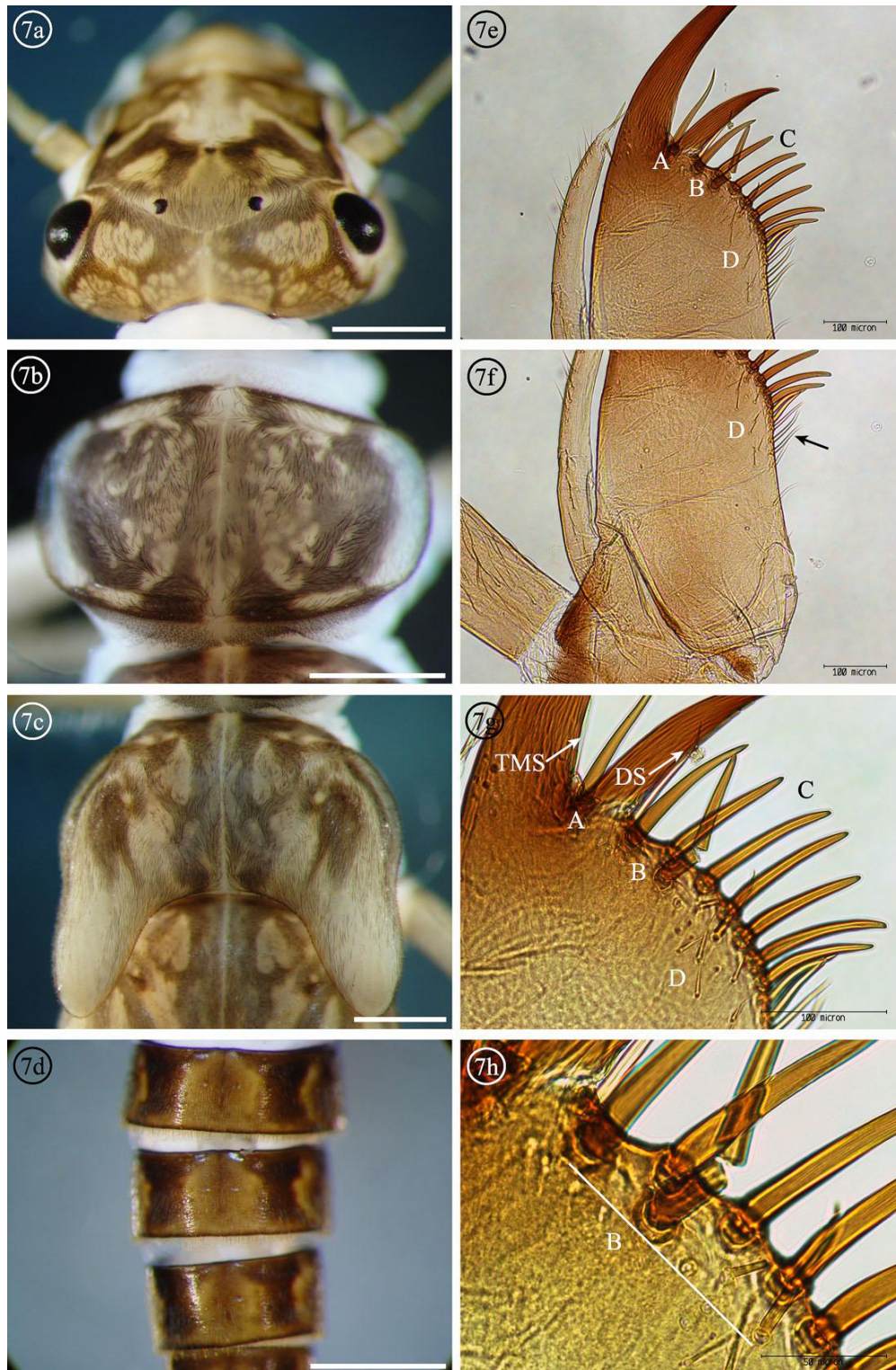
Isoperla denningi: Szczytko & Stewart 1979, 32:86-88.

Isoperla denningi: Szczytko & Stewart 2002, 128:6-7.
Larva (not reared).

Material examined. TYPE: *I. denningi*, Holotype ♂, CA: **Los Angeles Co.**, Monroe Canyon?, 4 mi W Tanbark Flats, 21/IV/1950, H.L. Hanson (CAS #8583). Paratype ♀, same location as Holotype, 21/IV/1950, H.L. Hanson (CAS). **Additional Specimens.** CALIFORNIA: **Los Angeles Co.**, Arroyo Sequit, Mulholland Dr., 1.5 mi (2.4 km) N Hwy 101, S of Solromar, 29/IV/2002, Larvae (ABL); Elizabeth Canyon Creek, Lake Hughes Rd., ~10 mi (16.1 km) E I-5, 1/V/2002, Larvae (ABL); ~0.6 mi (1.0 km) below Prospect Canyon, Winter 2003, Larvae, (ABL); Encinal Canyon Creek, ~ 0.5 mi (0.8 km) above mouth, T1, 4/VI/2008, Larvae (ABL); Little Rock Creek, Forest Service Route 5N04, ~0.4 mi (0.6 km) below Kitter Canyon Creek, R1, 15/V/2008, Larvae (ABL), **San Diego Co.**, Boulder Creek, Boulder Creek Rd., 13.9 mi (22.4 km) N Descanso, 01/V/2007, J. Sandberg, Larvae; Cañada Verde, Hwy 79 at Pacific Crest Trail, 1.1 mi (1.8 km) S Warner Springs, 10/V/2010, 15/VI/2010, Larvae (ABL); Carney Canyon Creek, Pamo Valley, 7.5 mi (12.1 km) N Ramona, 12/V/2010, Larvae (ABL); Cedar Creek, ~1.5 mi (2.4 km) above San Diego River, 12/V/2009, Larvae (ABL); Cold Stream, Hwy 79, 9.9 mi (15.9 km) N Hwy 8, near intersection with Pipeline Fire Rd., 03/V/2007, J. Sandberg, Larvae; Conejos Creek, at El Capitan

Reservoir, 14/IV/2008, Larvae (ABL); Cottonwood Creek, Downstream of Old Hwy 80 crossing, 04/V/2007, Larvae (ABL); De Luz Creek, De Luz Murrieta Rd., 2.9 mi (4.7 km) NE De Luz, 16-17/IV/2010, J. Sandberg, D. Pickard, Larvae (reared 1 male); Fry Creek, New Fry Creek Campground W side of Canfield Rd., 2.9 mi (4.7 km) N Cty Hwy S7 (6), 06/V/2008, J. Sandberg, D. Pickard, Larvae; Japacha Creek, above Hwy 79 crossing, 3.7 mi (5.9 km) S Paso Picacho Campground, 7.9 mi (12.7 km) N Hwy 8, 08/VI/2010, Larvae (ABL); Pine Creek, Pine Creek Road, 3.9 mi (6.3 km) N Pine Valley off Old Hwy 80, 02/V/2007, J. Sandberg, Larvae; Pine Valley Creek, ~1.6 mi (2.6 km) above Hwy 8, 01/VII/2006, Larvae (ABL); Pine Valley Creek, ~2.3 mi above Secret Canyon Creek, 05/V/2009, Larvae (ABL); Pine Valley Creek, Below Nobel Canyon Creek, 05/V/2009, Larvae (ABL); Roblar Creek, 0.36 mi (0.6 km) E Camp De Luz Rd. crossing, Camp Pendleton USMC, 18/IV/2008, J. Sandberg, Larvae (not reared); San Luis Rey River WE, 1 mi (1.6 km) N Mendenhall Valley, R1, 28/IV/2009, Larvae (ABL); San Mateo Creek, San Mateo Canyon, Tenaja Trail crossing at Tenaja Truck Trail & Los Alamos Rd., 05/V/2008, 16/IV/2010, J. Sandberg, D. Pickard, Larvae (rearing failed); Santa Ysabel Creek, at Hwy 79, 24/IV/2008, Larvae (ABL); Santa Ysabel Creek, Below Cleverger Canyon Creek, 29/IV/2009, Larvae (ABL); Stone Creek, 0.41 mi (0.7 km) upstream from S. Stagecoach Lane crossing, 06/V/2008, J. Sandberg, D. Pickard, Larvae (reared); Sweetwater River, Wildwood Glen Lane bridge, 0.1 mi (0.2 km) W Hwy 79 near Los Terrentos, 04/V/2007, J. Sandberg, Larvae; Temescal Creek, Pamo Road, 8 mi (12.9 km) N Ramona, N33.17601, W116.85052, 13/VI/2010, Larvae (ABL); Troy Canyon Creek, near Troy Flat off Kitchen Creek Rd., 3.6 mi (5.8 km) S Sunrise Hwy, 02/V/2007, J. Sandberg, Larvae; **Santa Barbara Co.**, Jalama Creek, Jalama Rd at railroad crossing, 2.5 mi W of Jalama Ranch, 06/V/2008, Larvae (ABL); La Brea Creek, FR 10N06 crossing, 3.6 mi (5.8 km) E Hwy 176 intersection, , Larvae (ABL); **Ventura Co.**, Cold Creek, Cold Creek Middle, Duplicate, 03/V/2010, Larvae (ABL).

Male larva. Body length of mature larva 11–12 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus usually not connected to



Figs. 7a-h. *Isoperla denningi* nymph, Roblar Creek, San Diego County and ventral maxilla, Jamala Creek, Santa Barbara County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 7e-f 100x, 7g 200x, and 7h 400x.

light frontoclypeus area, median longitudinal light band thin with parallel margins, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with completely enclosed small light areas along outer lateral margins; interocellar area variable, usually its entire area lighter than surrounding dark pigment, partially filled with indistinct light brown pigment, extending past posterior ocelli and connected to light area below occipital spinulae band, occasionally interocellar area partially filled with surrounding dark pigment and not connected to light area of posterior head capsule; occiput with irregular spinulae band extending from below eye to near median epicranial suture, partially enclosed by light brown pigment (Fig. 7a). **Lacinia** bidentate, total length 756–1093 μm (Figs. 2e, 7e-h, Tables 2-4); submarginal row (A+B) with 3–4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 7g); 1 submarginal seta (A) inserted at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal seta (A) or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 7g-h); 2–3 submarginal setae (B) located past SAT inner margin (Figs. 7g-h); 9–13 marginal setae (C) initially long-stout and widely spaced, last few shorter and widely spaced, sometimes borne from ventral or dorsal surface or broken with visible sockets (Fig. 7e); 11–34 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length and concentrated in apical half, occasionally a few setae located below submarginal row striated (Fig. 7f); dorsal surface setae (DSS) usually absent, sometimes last few marginal setae (C) form a short dorsal row (Fig. 7f – arrow). 15–25 minute scale-like spinulae on and along dorsal inner-lateral margin in basal half. **Galea** with 35–48 setae in thick ventral band, apex with 4–5 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with thin, median light area bordered by irregular dark longitudinal bands with adjacent light rugosities; discs each with dark comma shaped lateral areas and fine dark clothing setae restricted to areas

of dark pigmentation, lateral margins with broad light bands (Fig. 7b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 7c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surface; fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20e); tibia with faint transverse bands near proximal end. **Abdominal terga** with two distinct longitudinal dark stripes; wide light median longitudinal band bisected with indistinct light brown median pigment band; lateral pair of dark longitudinal stripes not extending to lateral margins; numerous fine light clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 7d).

Distribution. *Isoperla denningi* is the common *Isoperla* species distributed throughout southern California. Previous northern California records from Fresno, Placer, Tuolumne, Tehama and Trinity counties (Szczytko & Stewart 1979, 2002) were not confirmed in this study. Larvae and exuviae collected from Secret Ravine Creek, Placer County keyed to *I. marmorata*.

Diagnosis. The larval male lacinia of *I. denningi* is distinct from other *Isoperla* species with 1–4 submarginal (A+B) setae in that the dorsal lacinial surface has no fine setae (must focus down through ventral surface to see) and ventral surface setae (D) are concentrated on the apical half (Fig. 7f). The larval dorsal head pigment pattern is striking in this species, which has a well defined median longitudinal light band extending from the median base of the M shaped mark, almost reaching the anterior unpigmented frontoclypeus area (Figs. 7a-d).

Remarks. This species was usually the only *Isoperla* in streams within its range, but co-occurred in a few southern California streams with the following species: *I. acula*, *I. adunca*, and *I. mormona*. *Isoperla denningi* was the ubiquitous species south of Monterey, Kings, Tulare, and Inyo counties. Emergence occurred in April–June, was lightly extended, and was determined from adult collections and limited rearing.

Isoperla fulva Claassen
(Figs. 2f, 8a-h, 20f)

Isoperla fulva Claassen 1937, 69:80. Holotype ♂, Logan River, Cache Co., Utah.

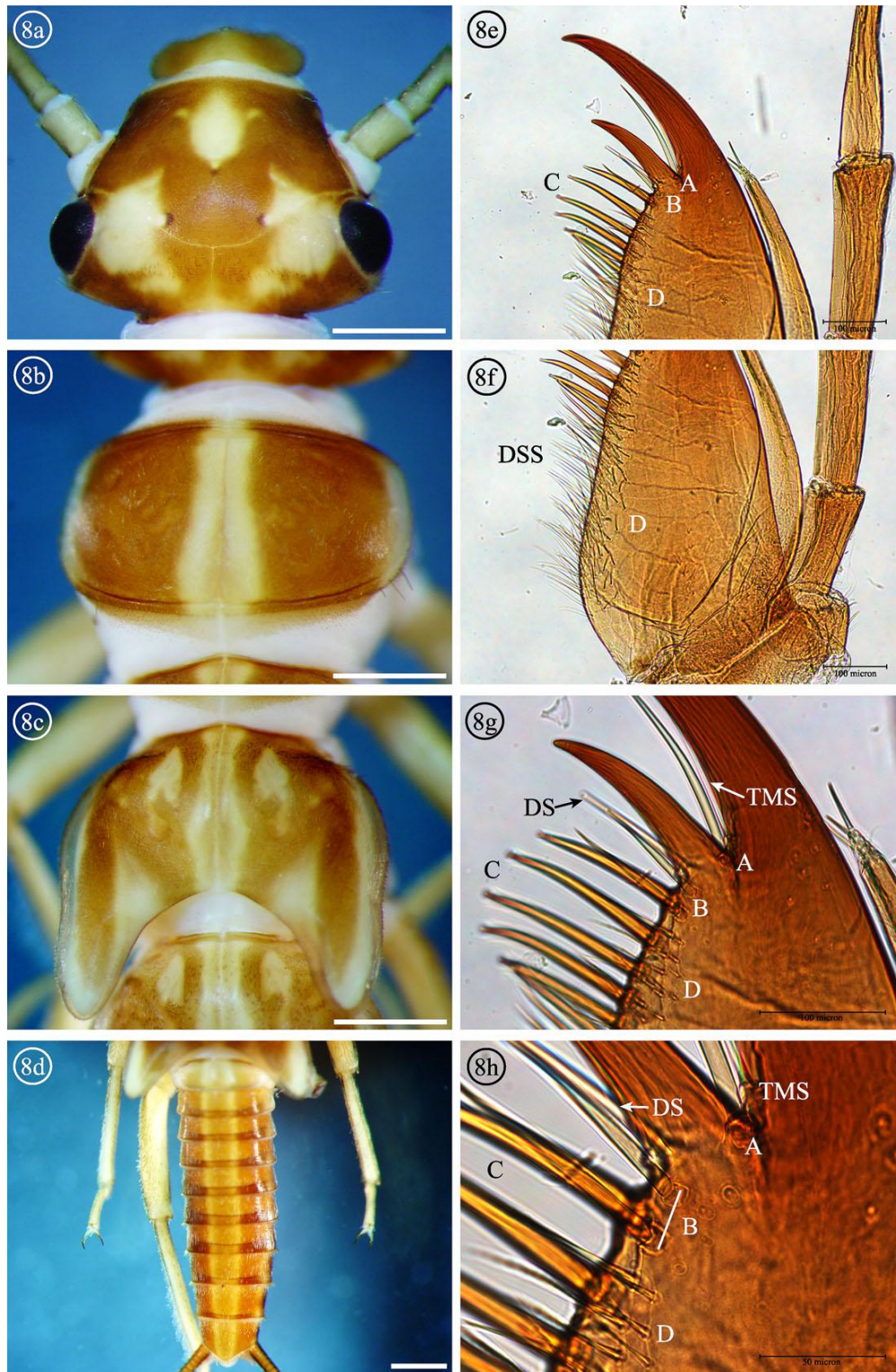
Isoperla fulva: Jewett 1960, 6:159. First California records.

Isoperla fulva: Szczytko & Stewart 1979, 32:67-75. ♂, ♀, larva (reared), ovum.

Material examined. COLORADO: **Boulder Co.**, SF Middle Boulder Creek, TR901, 3 mi (4.8 km) W Hessie, 6 mi (9.6 km) W Eldora, 23/VIII/1997, J. Sandberg, Larvae (reared); **Gunnison Co.**, Beaver Creek, at Beaver Creek Picnic Area near confluence with Gunnison River, 24/V/1997, J. Sandberg, Larvae (reared); Quartz Creek, Pitkin, The Ken & Francine Stewart Cabin, 07/VII/1999, J. Sandberg, ♂♀, Larvae (reared); **Larimer Co.**, Cache la Poudre River, 13/VI/1998, J. Sandberg, ♂♀, Larvae; **Saguache Co.**, Cochetopa Creek, Hwy 114 between UU-13 & 14-PP Roads, S of Hwy 50, 06/VI/2003, J. Sandberg, Larvae (reared); OREGON: **Douglas Co.**, Cow Creek, at Quines Creek, 08/IV/1968, S. Jewett Jr., ♂♀ not everted (NMNH); **Jackson Co.**, Applegate River, 10 mi (16.1 km) S Ruch, 22/V/1964, J. Schuh, ♂♀ (NMNH); **Jefferson Co.**, ?, Palisades State Park, 14/V/1954, S. Jewett Jr., ♂ (NMNH); **Klamath Co.**, Crescent Creek, Rt. 58, 39 mi (62.8 km) E Oakridge, 25/VI/1985, C. & O. Flint, Jr., ♀ (NMNH); Sprague River, near Bly, 02/VI/1972, D. Denning, ♂ (damaged) (NMNH); **Wallowa Co.**, Wallowa River, Wallowa Mts., Johnson Street Park, 02/VII/1948, C. Alexander, ♂♀, (poor condition) (NMNH); Wallowa River, Minam, 2700 feet, 21/VII/1929, H. Scullen, ♂ (NMNH); WASHINGTON: **Columbia Co.**, Tucannan River, Hwy 410 (12), 1940 feet, 20/IV/1968, E. Evans, ♂ (NMNH).

Male larva. **Body** length of mature larva 9–10 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus indistinct, not connected to light frontoclypeus area, median longitudinal light band usually oval, lateral thin arms variable, sometimes directed posterolaterally and extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins;

interocellar area variable, from completely dark to partially light and completely enclosed by dark pigment, light area not extending past posterior ocelli; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 8a). **Lacinia** bidentate, total length 688–829 μm (Figs. 2f, 8e-h, Tables 2-4); submarginal row (A+B) with 2–3 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Figs. 8g-h); 1 submarginal seta (A) inserted at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin sometimes obstructed from view by AT, submarginal seta (A) or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 8g-h); 1–2 submarginal setae (B) located past SAT inner margin (Fig. 8h); 6–11 marginal setae (C), initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal and ventral surface setae (Fig. 8e); 64–109 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 8f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 8f). **Galea** with 28–44 setae in thick ventral band, apex with 3–6 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area bordered by wide dark bands typical of the *I. marmorata* group; discs each with light rugosities, irregular median dark margins and fine dark clothing setae, lateral margins with broad light bands (Fig. 8b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 8c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surface; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20f); tibia with very faint transverse bands near proximal end. **Abdominal terga** with two distinct longitudinal dark stripes; wide light median longitudinal band bisected with



Figs. 8a-h. *Isoperla fulva* nymph and ventral maxilla, Beaver Creek, Gunnison County, CO. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 8e-f 100x, 8g 200x, and 8h 400x.

indistinct light brown median pigment band; lateral pair of dark longitudinal stripes usually not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 8d).

Distribution. Canada: Alberta, British Columbia. USA: Arizona, California?, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (Szczytko & Stewart 1979). The California listing was not confirmed during this study but adults need to be reared from Eagle Creek in the western Warner Mountains of Modoc County.

Diagnosis. The male larvae of *I. fulva* are most similar to other western species of the *I. marmorata* complex. They all share dark pigmented bodies and the pronotum is almost completely dark except for the median light band and lateral margins (Figs. 8, 10, 16a-d). The lacinia of these species is also similar. The larvae of *I. fulva* larvae are inseparable from *I. roguensis* (Figs. 16a-h & 20n), but both can be distinguished from *I. marmorata* by the lack of a median longitudinal light band connecting the light M shaped pattern to the unpigmented frontoclypeus (Fig. 8a).

Remarks. This species was not collected during this study from California. Eagle Creek, a Modoc County stream may contain this species; however, to confirm this, rearing is required.

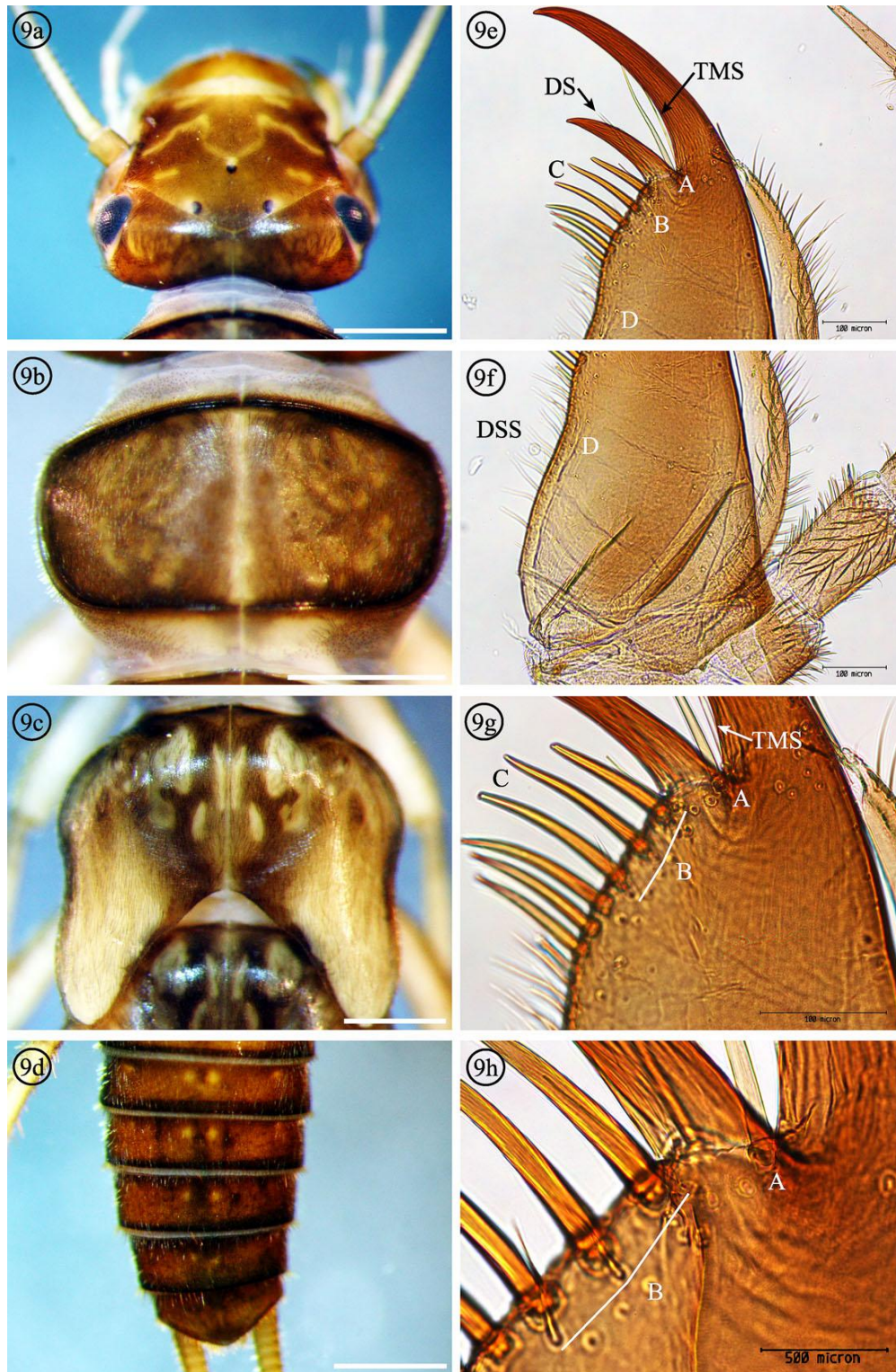
Isoperla laucki Baumann & Lee
(Figs. 2g, 9a-h, 20g)

Isoperla laucki Baumann & Lee 2009, 5:2-5. ♂, ♀, larva (reared), ovum.

Material examined. CALIFORNIA: **Humboldt Co., Dragsaw Spring**, FR 13N02 crossing, 12-13/VII/2009, 10-12/VII/2010, J. Sandberg, Larvae (reared).

Male larva. Body length of mature larva 9–10 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus a distinct thin band, not connected to light frontoclypeus area, median longitudinal light band absent, lateral thin arms directed posterolaterally, extending to antennal

bases; posterior ocelli with completely enclosed small light areas along outer lateral margins; interocellar area entirely dark; occiput with irregular spinulae band extending from below eye to near median epicranial suture, usually enclosed completely by dark pigment (Fig. 9a). **Lacinia** bidentate, total length 839–938 µm (Figs. 2g, 9e-h, Tables 2-4); submarginal row (A+B) with 4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 9g); 1–2 submarginal setae (A), the first located at base of apical tooth (AT) inner margin, the second when present, located between the AT and SAT inner margins, shorter and half as stout at base than first, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal seta (A) or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT (Figs. 9g-h); 2–3 submarginal setae (B) located past SAT inner margin (Fig. 9h); 7–9 marginal setae (C), initially long-stout and widely spaced, last few shorter and widely spaced, blending into and difficult to differentiate from dorsal surface setae (Fig. 9e); 8–13 ventral surface setae (D) scattered below marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, mostly concentrated in posterior half (Fig. 9f); dorsal surface setae (DSS) continue from last marginal setae (C) as a single, laterally protruding, submarginal row (sometimes 2–3 setae thick) along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 9f). **Galea** with 28–44 setae in thick ventral band, apex with 4–7 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with thin median light line bordered by irregular dark longitudinal bands with adjacent light rugosities; discs each with dark comma shaped lateral areas, fine dark clothing setae restricted to areas of dark pigmentation and lateral margins without broad light bands (Fig. 9b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 9c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surface; fine silky setae sparse on dorsal surfaces of femora and tibia (Fig. 20g); tibia with faint transverse bands near proximal end. **Abdominal terga** without distinct longitudinal dark



Figs. 9a-h. *Isoperla laucki* nymph and ventral maxilla, Dragsaw Spring, Humboldt County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 9e-f 100x, 9g 200x, and 9h 400x.

stripes; tergites marked with a close set pair of dorsal small light spots and a wide set triplet of light spots laterally; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 9d).

Distribution. Known only from four Humboldt County streams (Bauman & Lee 2009).

Diagnosis. Male larvae of *I. laucki* can be distinguished from other western *Isoperla* species with 1–2 submarginal setae (A) by the presence of 8–13 ventral lacinia surface setae (Figs 9e-h), fine silky setae sparse on dorsal surfaces of femora and tibia, the interocellar area completely dark (Fig. 9a), and abdomen lacking longitudinal stripes (Fig. 9d). This species is most similar to *I. adunca* (Figs. 4a-h & 20b) in that it lacks abdominal stripes (Fig. 9d), but can be separated by the interrupted lacinia submarginal setae row (Fig. 9g).

Remarks. This species was the only *Isoperla* species in four Humboldt County spring fed streams (Baumann & Lee 2009).

Isoperla marmorata Needham & Claassen
(Figs. 2h, 10a-h, 20h)

Isoperla marmorata Needham & Claassen 1925, 2:142.
Holotype ♀, Reno, Washoe Co., Nevada.

Isoperla marmorata: Szczytko & Stewart 1979, 32:62-67.
♂, ♀, larva (reared), ovum.

Material examined. CALIFORNIA: **Butte Co.**, ?, 9 mi (14.5 km) N Oroville, 24/IV/1955, S. Hitchcock, Larvae (NMNH); ?, Chico, 23/IV/1923, E. VanDuzee, ♂ (NMNH); **Big Chico Creek**, CSU-Chico near Holt Hall, 29/III/2007, 08/IV/2008, J. Sandberg, ♂♀; **Big Chico Creek**, Five-Mile Recreation Area, Centennial Ave. & Crow Canyon Ct., 27/III/2010, J. Sandberg, Larvae (reared); **Butte Creek**, 400 meters upstream from Doe Mill Road bridge, 28/V/2006, J. Sandberg, D. Pickard, Larvae (reared); **Butte Creek**, Butte Creek Ecological Reserve, Honey Run Rd., 2.9 mi (4.7 km) E intersection with Skyway, 11/III/2010, J. Sandberg, J. York, Larvae (reared); **Mud Creek**, Richardson Springs, 15/IV/2010, J. Sandberg, D. Pickard, J. York, Larvae (reared); **Contra Costa Co.**, ?, near Moraga, 26/IV/1966, D. Denning, ♀ (poor condition) (NMNH); **El Dorado Co.**, **Deadman Creek**, Church

Mine Rd. crossing, 2.45 mi (3.9 km) SE El Dorado, 05/IV/2009, J. Sandberg, A. Richards, Larvae (reared); **Greenwood Creek**, Greenwood Creek Park, Hwy 49, 4 mi (6.4 km) E Pilot Hill, 28/III/2009, 11/IV/2009, J. Sandberg, Larvae (reared); **Martinez Creek**, Martinez Creek Rd., 3.5 mi (5.6 km) SE El Dorado, 04/IV/2009, J. Sandberg, D. Pickard, Larvae (reared); **NF Cosumnes River**, Hwy 49 Nashville, 31/V/1982, R. Bottorff, ♀ (NMNH); **NF Cosumnes River**, Hwy 49 cattle corral, 1.7 mi (2.7 km) S Nashville below confluence with MF Cosumnes River, 28/IV/2007, 28/III/2009, 30/III/2009, 11/IV/2009; J. Sandberg, 05/IV/2009; J. Sandberg, A. Richards, 11/IV/2009; J. Sandberg, Larvae (reared); **Weber Creek**, Forni Road bridge crossing at Placerville, 28/III/2009, J. Sandberg, Larvae (reared); **Humboldt Co.**, **Mad River**, Arcata Bottoms, Mad River Rd., N40.91578° W124.10618°, 10/IV/2010, J. Sandberg, ♀; **Nevada Co.**, **Sagehen Creek**, at diversion structure, 6300 feet, 18/VI/1965, A. Sheldon, ♀ (NMNH); **Placer Co.**, **Secret Ravine**, Rocklin Road bridge crossing at Rocklin, 11/IV/2008, J. Sandberg, A. Richards, Larva; **Plumas Co.**, **Domingo Spring**, Domingo Springs Campground, 8.5 mi (13.7 km) NW Chester on Old Red Bluff Rd., 13/VI/2007, 03/VII/2010, J. Sandberg, ♂♀; **Sacramento Co.**, **Cosumnes River**, Michigan Bar, 23/IV/1982, R. Bottorff, Exuviae (NMNH); **Cosumnes River**, Michigan Bar, 18/IV/1986, R. Bottorff, ♂♀ damaged (NMNH); **Siskiyou Co.**, **McCloud River**, Middle Falls near Fowlers Campground, 5.5 mi (8.8 km) E McCloud (Hwy 89), 13/V/2007, J. Sandberg, D. Pickard, ♂; **Tehama Co.**, **Big Chico Creek**, Hwy 32 bridge, 2.3 mi (3.7 km) N of Lomo & Humboldt Rd. intersection, 06/I/2007, J. Sandberg, A. Richards, Larva; 03/IV/2010, J. Sandberg, Larvae (reared dark variant); **Pine Creek**, Wurlitzer Ranch, Barber Rd., 1.5 mi (2.4 km) E Meridian Rd. intersection, 07/III/2007, 03/III/2008, 03/III/2010, J. Sandberg, D. Pickard, Larvae (reared); **SF Calf Creek**, Hwy 32 crossing, 2.75 mi (4.4 km) S Potato Patch Campground, 26/IV/2010, R. Baumann, B. Kondratieff, A. Richards, J. Sandberg, J. Slusark, Larvae (reared); **Trinity Co.**, **SF Trinity River**, Hwy 36, Forest Glen Campground, Forest Glen, J. Sandberg, 22/V/2008, Exuviae. OREGON: **Benton Co.**, **Rock Creek**, 4 mi (6.4 km) W Philomath, 27/IV/1963, T. Schuh, ♀ (NMNH); **Clatsop Co.**, **Nehalem River**, at Red Bluff Rd., 4 mi (6.4 km) NE Elsie, 17-18/IV/1965, S. Jewett Jr., ♂ (NMNH);

Columbia Co., Scappoose Creek, ?location, 08/V/1948, S. Jewett Jr., ♀ (NMNH); **Jackson Co.**, Squaw Lake, ?location, 22/V/1964, J. Schuh, ♂ (NMNH); **Linn Co.**, Stream near CAP. III Monument Peak, 16/VII/1960, ?collector, ♀ (NMNH).

Male larva. Body length of mature larva 11–13 mm.

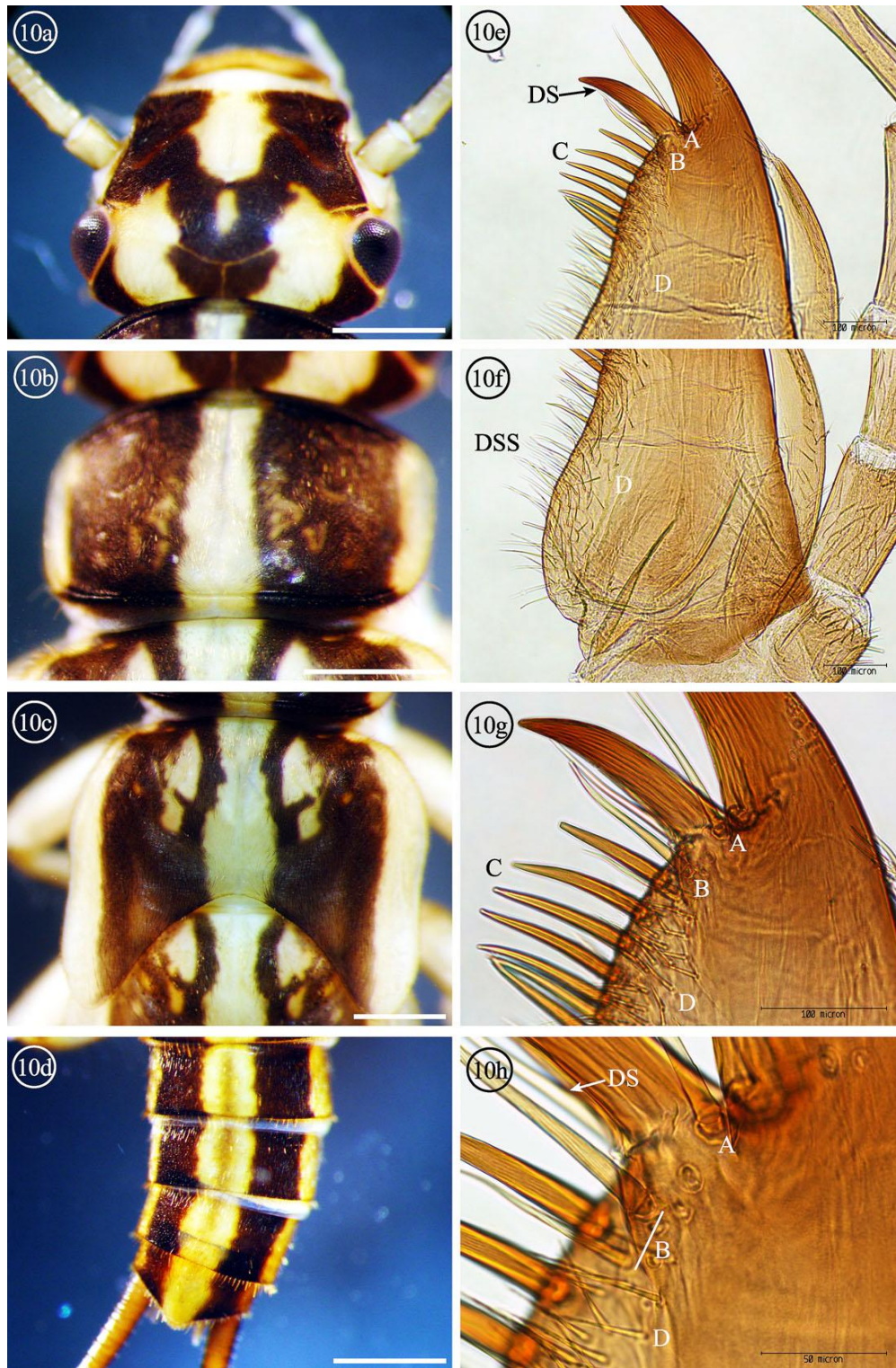
Dorsum of head with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus indistinct, connected (sometimes partially) to light frontoclypeus area by a wide median longitudinal light band, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area variable, usually partially light, completely enclosed by dark pigment and not extending past posterior ocelli; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 10a). **Lacinia** bidentate, total length 816–974 µm (Figs. 2h, 10a-h, Tables 2-4); submarginal row (A+B) with 2–3 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 10g); 1 submarginal seta (A) inserted at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal seta (A) or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 10g-h); 1–2 submarginal setae (B) located past SAT inner margin (Fig. 10h); 7–10 marginal setae (C), initially long-stout and widely spaced, last few shorter and variably spaced, blending into and difficult to differentiate from dorsal and ventral surface setae (Fig. 10e); 72–110 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 10f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 10f). **Galea** with 19–40 setae in sparse ventral row, apex with 4–5 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area bordered by wide dark bands

typical of the *I. marmorata* complex; discs each with light rugosities concentrated along median dark margins and fine dark clothing setae, lateral margins with broad light bands (Fig. 10b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 10c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surface; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20h); tibia with faint transverse bands near proximal end. **Abdominal terga** variable, usually with two distinct longitudinal dark stripes; wide light median longitudinal band sometimes bisected with faint, light brown longitudinal stripe; lateral pair of dark longitudinal stripes usually not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 10d).

Distribution. California, Nevada, Oregon, and Washington. In northern California, this species was found in small to medium sized creeks and rivers at a variety of elevations. It occurred with *I. acula*, *I. mormona*, *Isoperla pinta* Frison, *Isoperla quinquepunctata* (Banks), and *I. roguensis*.

Diagnosis. Male larvae of the *I. marmorata* complex were differentiated from other species with 1–2 lacinia submarginal (A) setae by having 41–110 ventral surface setae and pronotal discs mostly dark. Within the complex, *I. marmorata* was distinguished from *I. roguensis* by usually having the light M shaped pattern connected to the light anterior frontoclypeus area by a light longitudinal band (See also diagnosis under *I. fulva*). The only exception to the light M shaped pattern character occurred in 8 exuviae collected from Prairie Creek, Humboldt County, California. These possessed partial to entire M shaped light patterns, but were not connected to the light anterior frontal clypeus area.

Remarks. In Big Chico Creek, this species was collected at 82.9 m elevation, at Five-mile Recreation Area, Chico, and at 1043.9 m elevation at the Hwy 32 crossing, 45.1 km north of Chico. The adults of these two locations had different pigment patterns; the low elevation population was lighter than the high elevation darker population. A black adult *I.*



Figs. 10a-h. *Isoperl*a *marmorata* nymph and ventral maxilla, Greenwood Creek, El Dorado County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, and Dorsal seta DS. White bars = 1 mm, 10e-f 100x, 10g 200x, and 10h 400x.

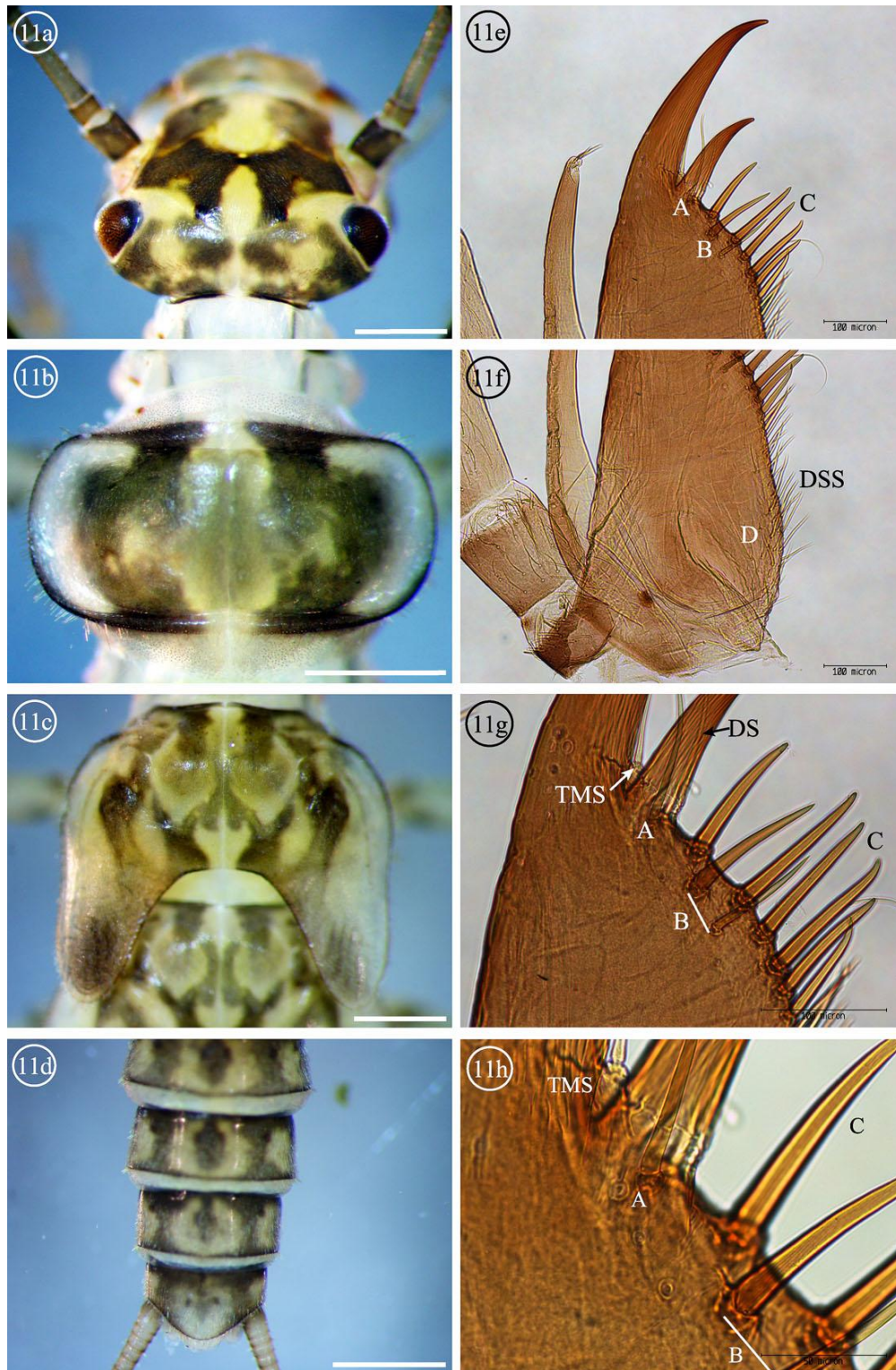
marmorata variant has also been collected from Prairie Creek, Humboldt County (J.J. Lee, pers. com.). These “dark and black” variant color morphs have been suggested to be either ecophenotypes or cryptic sibling species within *I. marmorata* and more studies are needed to address this observation. Emergence occurred in April–May and the black Prairie Creek, Humboldt County population began its emergence in March (J.J. Lee, pers. com.).

Isoperla miwok Bottorff & Szczytko
(Figs. 2i, 11a-h, 20i)

Isoperla miwok Bottorff & Szczytko 1990, 92:287-291. ♂, ♀, larva (reared), ovum.

Material examined. TYPES: *I. miwok*, Holotype ♂, Allotype ♀, CA: **El Dorado Co.**, 3.3 km NE Michigan Bar bridge, 5.3 km SW Latrobe, Indian Creek, 13/IV/1987, R.L. Bottorff (NMNH #104427). **Additional Specimens.** CALIFORNIA: **Butte Co.**, Campbell Creek & tributary, North Table Mountain Wildlife Area, Cherokee Rd, 5 mi (8 km) S Cherokee, 09/II/2007, 17/II/2007, J. Sandberg, Larvae; 03/III/2007, J. Sandberg, A. Richards, Larvae; 07/IV/2007, 13/IV/2007, J. Sandberg, ♀, Larvae (reared); 18/IV/2007, J. Sandberg, ♂; 02/II/2008, 09/II/2008, J. Sandberg, Larvae; 23/II/2008, J. Sandberg, D. Pickard, Larvae; 08/III/2008, 17/III/2008, 24/III/2008, 30/III/2008, J. Sandberg, Larvae (reared); Campbell Creek & tributary, North Table Mountain Wildlife Area, Cherokee Rd, 5.6 mi (9 km) S Cherokee, 5-6/IV/2008, J. Sandberg, ♂♀; 08/IV/2008, J. Sandberg, Larvae; 27/IV/2010, R. Baumann, B. Kondratieff, J. Sandberg, ♂; 02/V/2010, J. Sandberg, A. Richards, ♂♀, Larvae; 12/III/2011, J. Sandberg, ♂, Larvae (reared); 27/III/2011, J. Sandberg, Larvae (reared); Oregon Gulch, Red Bridge at Oregon Gulch Road, Oregon City, 16/III/2008, 22/III/2008, J. Sandberg, Larvae; 27/IV/2010, R. Baumann, B. Kondratieff, J. Sandberg, ♂♀; 02/V/2010, J. Sandberg, A. Richards, ♂♀, Larvae (reared); **El Dorado Co.**, Tributary of NF Cosumnes River, Union Mine Rd., 3.4 mi (5.5 km) N Nashville at McNulty Mine Rd. crossing, 04/IV/2009, J. Sandberg, D. Pickard, Larvae; 25/IV/2009, J. Sandberg, Larvae (reared); **Lake Co.**, ?, S junction Hwy 20 & 53, 22/IV/1955, S. Hitchcock, Larvae (lacinia mounted – Slide #007) (NMNH).

Male larva. Body length of mature larva 9–11 mm. **Dorsum of head** with contrasting pigment pattern and fine light clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus variable, usually connected to light frontoclypeus area by an apically narrowed median longitudinal light band, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area variable, usually partially light, completely enclosed by dark pigment and extending posteriorly to epicranial Y-suture or sometimes open posteriorly and connected to posterior margin of head by thin light longitudinal band; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 11a). **Lacinia** bidentate, total length 622–888 μm (Figs. 2i, 11e-h, Table 2-4); submarginal row (A+B) with 2–3 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 11g); 1 submarginal seta (A) inserted near mid-base of SAT, half as stout at its base as first submarginal (B) seta, plus 1 thin marginal seta (TMS) adjacent to apical tooth (AT) inner margin, sometimes obstructed from view by AT or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT (Figs. 11g-h); 1–2 submarginal setae (B) located past SAT inner margin (Fig. 11h); 5–7 marginal setae (C), initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 11e); 7–15 ventral surface setae (D), scattered below marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length and concentrated in posterior half (Fig. 11f); dorsal surface setae (DSS) continue from last marginal setae (C) as a single, laterally protruding, submarginal row (sometimes 2–3 setae thick) along inner-lateral margin, ending before or near posterior-most ventral surface setae (Fig. 11f); 10–15 minute scale-like spinulae rarely present on and along ventral inner-lateral margin at middle of lacinia. **Galea** with 12–26 setae in sparse ventral row, apex with 2–4 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with large median light area bordered by thick dark comma shaped bands (typical of the *I.*



Figs. 11a-h. *Isoperla miwok* nymph and ventral maxilla, Tributary of Campbell Creek, Butte County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal seta DS, Thin marginal seta TMS. White bars = 1 mm, 11e-f 100x, 11g 200x, and 11h 400x.

sobria complex) that fade rapidly in alcohol; discs each with fine light clothing setae, except over small light rugosities and lateral margins with broad light bands (Fig. 11 b); **Meso and metanotum** with contrasting pigment pattern and fine light clothing setae (Fig. 11c). **Legs** with numerous fine light clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surface; fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20i); distal femora and proximal tibia with faint transverse bands. **Abdominal terga** with three distinct longitudinal dark stripes; wide median longitudinal light band bisected with thin dark median longitudinal stripe; lateral pair of dark longitudinal stripes about as wide as median dark stripe, not extending to lateral margins; numerous fine light clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 11d).

Distribution. California: usually non-perennial central Sierra Nevada foothill creeks.

Diagnosis. Male larvae of *I. miwok* are distinctive among all other California *Isoperla* species with 2–4 total submarginal (A+B) setae by the single lacinia submarginal (A) seta arising from near the middle of the base of the subapical tooth (Fig. 11h).

Remarks. *Isoperla miwok* has long antennae and cerci as noted by Bottorff et al. (1990) which often break when collected and pigment patterns that darken or fade when preserved in ethanol. This species was collected with and emerged slightly before *I. adunca* from non-perennial foothill streams usually containing submerged aquatic plants. In Campbell Creek, Butte County, a large population seems to tolerate the increased organic enrichments supplied by ranging cattle and medium levels of stream bank erosion. Emergence occurred in late March–early May (late May in wetter years).

Isoperla mormona Banks
(Figs. 2j, 12a-h, 20j)

Isoperla mormona Banks 1920, 64:332. Holotype ♀, Vinyard, Utah.

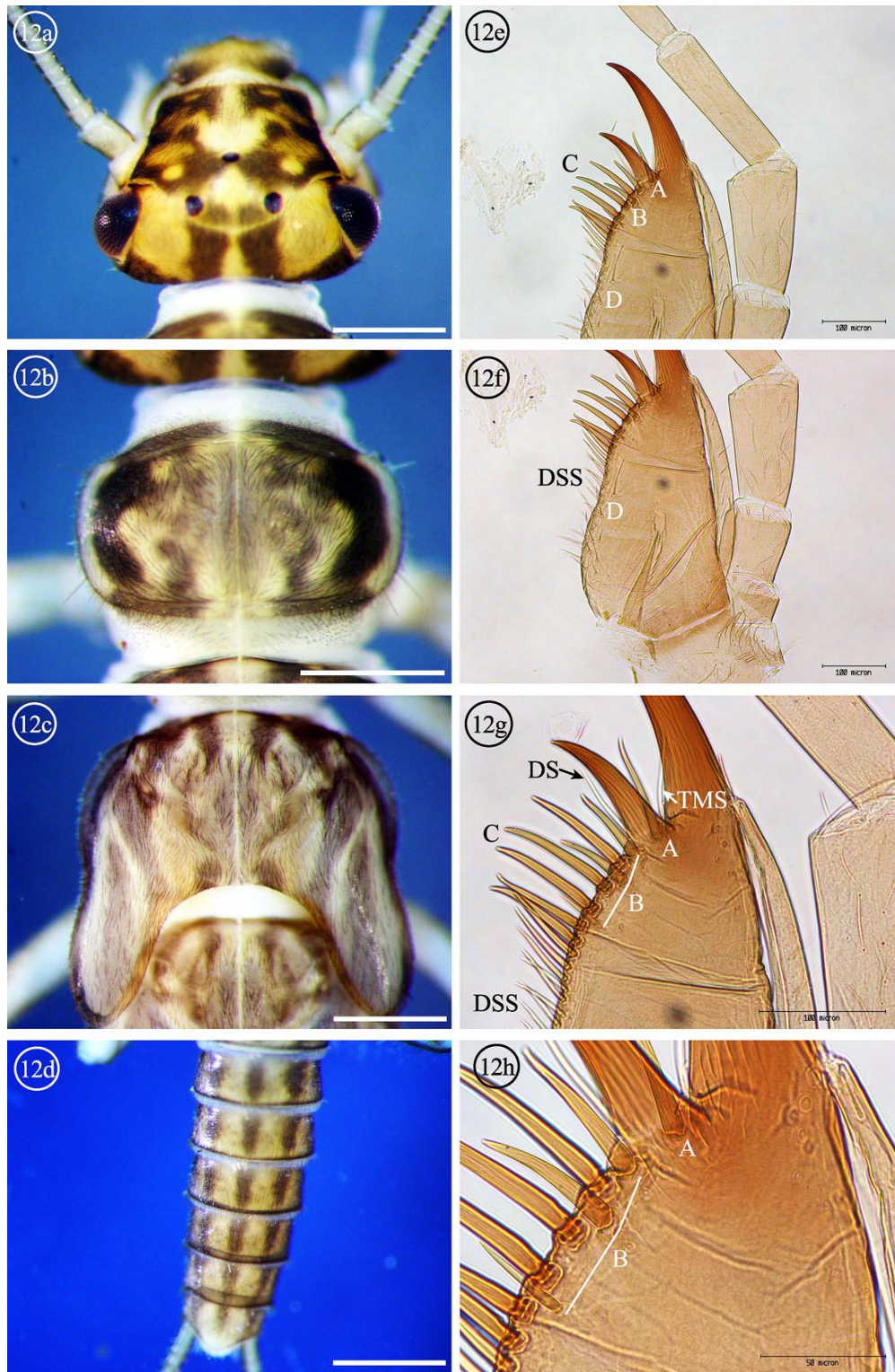
Isoperla mormona: Szczytko & Stewart 1979, 32:23-27. ♂, ♀, larva (reared), ovum.

Materials Examined. CALIFORNIA: **Alameda Co.**, ?, Sunol Regional Park, 24/IV/1971, D. Denning, ♂ (NMNH); **Indian Creek**, 1.8 mi (2.9 km) upstream of San Antonio Reservoir, 25-V-2010, Larva (ABL); **Butte Co.**, **Big Chico Creek**, Hooker Oak Recreation Area Chico, 10/V/1968, E. Evans, ♀ (NMNH); **Big Chico Creek**, Big Chico Creek Ecological Reserve, N39.86909 W121.70760, near north boundary, 24/V/2009, J. Sandberg, A. Richards, ♂♀, Larvae (reared); 25/V/2009, J. Sandberg, D. Pickard, Larvae; **Big Chico Creek**, Five-Mile Recreation Area, Centennial Ave & Crow Canyon Ct, Chico, (11, 15, 19)/V/2010, J. Sandberg, ♂♀, Larvae (reared); Creek?, Richardson Springs, 11/V/1968, E. Evans, D. Maddox, ♂ (NMNH); **Mud Creek**, Richardson Springs, 15/IV/2010, J. Sandberg, D. Pickard, J. York, Larvae; **El Dorado Co.**, **Deadman Creek**, Church Mine Road crossing, 2.45 mi (3.9 km) SE El Dorado, 23/V/2009, J. Sandberg, Larvae (1♂ reared); **Greenwood Creek**, Greenwood Creek Park, Hwy 49, 4 mi (6.4 km) E Pilot Hill, 16/V/2008, J. Sandberg, ♂♀; 28/III/2009, Larvae; 25/IV/2009, Larvae; 10/V/2009, ♀; 16/V/2009, 23/V/2009, ♂, Larvae (reared); **NF Cosumnes River**, Hwy 49 Nashville, 11/VI/1982, 13-19/VI/1982, R. Bottorff, ♂♀ (NMNH); **NF Cosumnes River**, Sweenys, Somerset, 23/VI/1952, R. Bottorff, ♀ (NMNH); **Weber Creek**, Forni Road bridge crossing Placerville, 16/V/2008, J. Sandberg, ♀; **Inyo Co.**, ?, Sawmill, 3800 feet (1158 m), W Hwy 395, 15/VII/1965, A. Sheldon, ♂♀ (NMNH); **Kern Co.**, **Lucas Creek**, Breckenridge Mt FR Rd, 5.7 mi S Hwy 178 nr Democrat Hot Springs, 10/IV/2008, Larvae (ABL); **Los Angeles Co.**, **Little Rock Creek**, Cheseboro Rd (Forest Service Rd 5N04), 10.5 mi (16.9 km) S Littlerock, 03/VI/2010, Larvae (ABL); **Marin Co.**, ?, Muir Woods, 27/VI/1965, D. Denning, ♂♀ (NMNH); Creek?, Near Point Reyes, 11/V/1971, D. Denning, ♂ (NMNH); **Paper Mill Creek**, ?location, 06/VI/1965, S. Jewett Jr., ♀ (NMNH); **Modoc Co.**, ?, 8 mi (12.9 km) NW Fandango Pass, Warner Mts, 11/VII/1967, Adult, E. Evans (NMNH); **Thomas Creek**, ~2.8 mi (4.5 km) below Hwy 299, 29/VI/2004, Larvae (ABL); **Monterey Co.**, **Big Sur River**, Pfeiffer Big Sur State Park, 12/VII/1958, C. Alexander, ♀ (NMNH); **Napa Co.**, ?, 7.6 mi (12.2 km) W Hwy 121 on Hwy 128, 20/VI/1985, C. & O. Flint Jr., Larvae (NMNH); Creek?, Near Glen Ellen, 18/V/1974, D. Denning, ♂ (NMNH); **Plumas Co.**, **Grizzly Creek**, 2 mi (3.2 km) below Lake Davis

Dam, 23/V/2006, J. Sandberg, D. Pickard, J. Slusark, ♂♀; Spanish Creek, Spanish Creek Campground, 3 mi (4.8 km) N of Keddie, 02/VII/2006, J. Sandberg, J., M., E., and S. Hartway, ♂♀, Exuviae; Spanish Creek, Chandler Road bridge, 13/XI/2007, Larvae (ABL); **Sacramento Co.**, Cosumnes River, Sloughhouse, 31/V/1982, 14/VI/1982, R. Bottorff, ♀ (NMNH); Cosumnes River, Michigan Bar, 06/VII/1982, R. Bottorff, ♂♀ (NMNH); **San Bernardino Co.**, Deep Creek, ~0.9 mi (1.4 km) above Crab Creek, 03/VI/2009, Larvae (ABL); Mill Creek, ~0.3 mi (0.5 km) W Mill Creek Campground, 15/V/2002, Larvae (ABL); SF Santa Ana River, E Barton Flats, 6200 feet (1890 m), San Bernardino Mts., 3-5/VII/1958, C. Alexander, ♂♀ (NMNH); **San Mateo Co.**, Gazos Creek, Gazos Creek Road near Hwy 1, 10/IV/2007, Larvae (ABL); **San Luis Obispo Co.**, San Simeon Creek, at San Simeon Creek Rd, 22/IV/2009, Larvae (ABL); **Santa Cruz Co.**, San Lorenzo River, HC Redwoods State Park, Hwy 9, 0.5 mi (0.8 km) S Felton, 24/V/2007, J. Sandberg, Exuviae; **Shasta Co.**, ?, Burney, 19/VI/1963, C. Quick, ♂♀ (NMNH); Burney Creek, ~1.7 mi (2.7 km) below Burney Falls, 16/VI/2004, Larvae (ABL); **Sierra Co.**, Little Truckee River, Hwy 89 crossing, 12 mi (19.3 km) S of Sierraville, 21/VII/1950, C. Alexander, ♀ (NMNH); **OREGON: Benton Co.**, ?, 9 mi (14.5 km) W Berry Creek Experimental Station, Corvallis, 07/VI/1968, E. Evans, ♂ (NMNH); **Crook Co.**, ?, Ochoco Forest Campground nr Prineville, 26/VII/1963, J. Baker, ♀ (NMNH); **Klamath Co.**, ?, Klamath Falls, Black Light, 15/VII/1971, J. Schuh, ♀ (NMNH); **Umatilla Co.**, Umatilla River?, near Rieth, 05/VII/1948, C. Alexander, ♂♀ (NMNH); **WASHINGTON: Yakima Co.**, Naches River, near Naches, 31/VII/1947, C. Alexander, ♀ damaged (NMNH).

Male larva. Body length of mature larva 7–9 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus connected to light frontoclypeus area by a thin median longitudinal light band, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area variable, usually partially light, completely enclosed by dark pigment with light area extending to posterior margin of posterior

ocelli, or sometimes mostly light and connected to posterior margin of head capsule by a thin median light band; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 12a). **Lacinia** bidentate, total length 525–666 µm (Figs. 2j, 12e-h, Tables 2-4); submarginal row (A+B) with 4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 12g); 1 submarginal seta (A) inserted at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT (Figs. 12g-h); 3 submarginal setae (B) located past SAT inner margin (Fig. 12h); 6–9 marginal setae (C), initially long-stout and widely spaced, last few shorter and widely spaced, blending into and difficult to differentiate from dorsal surface setae (Fig. 12g); 7–14 ventral surface setae (D) scattered below marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length and concentrated in posterior half (Fig. 12f); dorsal surface setae (DSS) continue from last marginal setae (C) as a single, laterally protruding, submarginal row (sometimes 2–3 setae thick) along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 12f). **Galea** with 12–17 setae in sparse ventral row, apex with 2–3 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area bordered (at least partially) by thin, irregular dark bands; discs each with partially enclosed light areas or “windows”, fine dark clothing setae and lateral margins with broad light bands (Fig. 12b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 12c). **Legs** with numerous fine dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20j); tibia with faint transverse bands near proximal end. **Abdominal terga** with three distinct longitudinal dark stripes; wide light median longitudinal band bisected with thin dark median longitudinal stripe; lateral pair of dark longitudinal stripes about as wide as median dark stripe, not extending to lateral margins;



Figs. 12a-h. *Isoperla mormona* nymph and ventral maxilla, Greenwood Creek, El Dorado County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae DSS, Dorsal Seta DS, and Thin marginal seta TMS. White bars = 1 mm, 12 e-f 100x, 12g 200x, and 12 h 400x.

numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 12d).

Distribution. Canada: British Columbia. USA: Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, and Wyoming. Mexico: Baja California. Widely distributed throughout California.

Diagnosis. Mature *I. mormona* male larvae are the smallest western *Isoperla* species (7–9 mm) and can be separated from other similar species that possess 2–4 submarginal setae (A+B) by having 7–14 ventral surface (D) setae (Fig. 12f), fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20j) and interocellar area partially light (Fig. 12a).

Remarks. *Isoperla mormona* is distributed throughout northern and southern California from perennial and non-perennial streams. In Butte and El Dorado counties, emergence occurred in May–June.

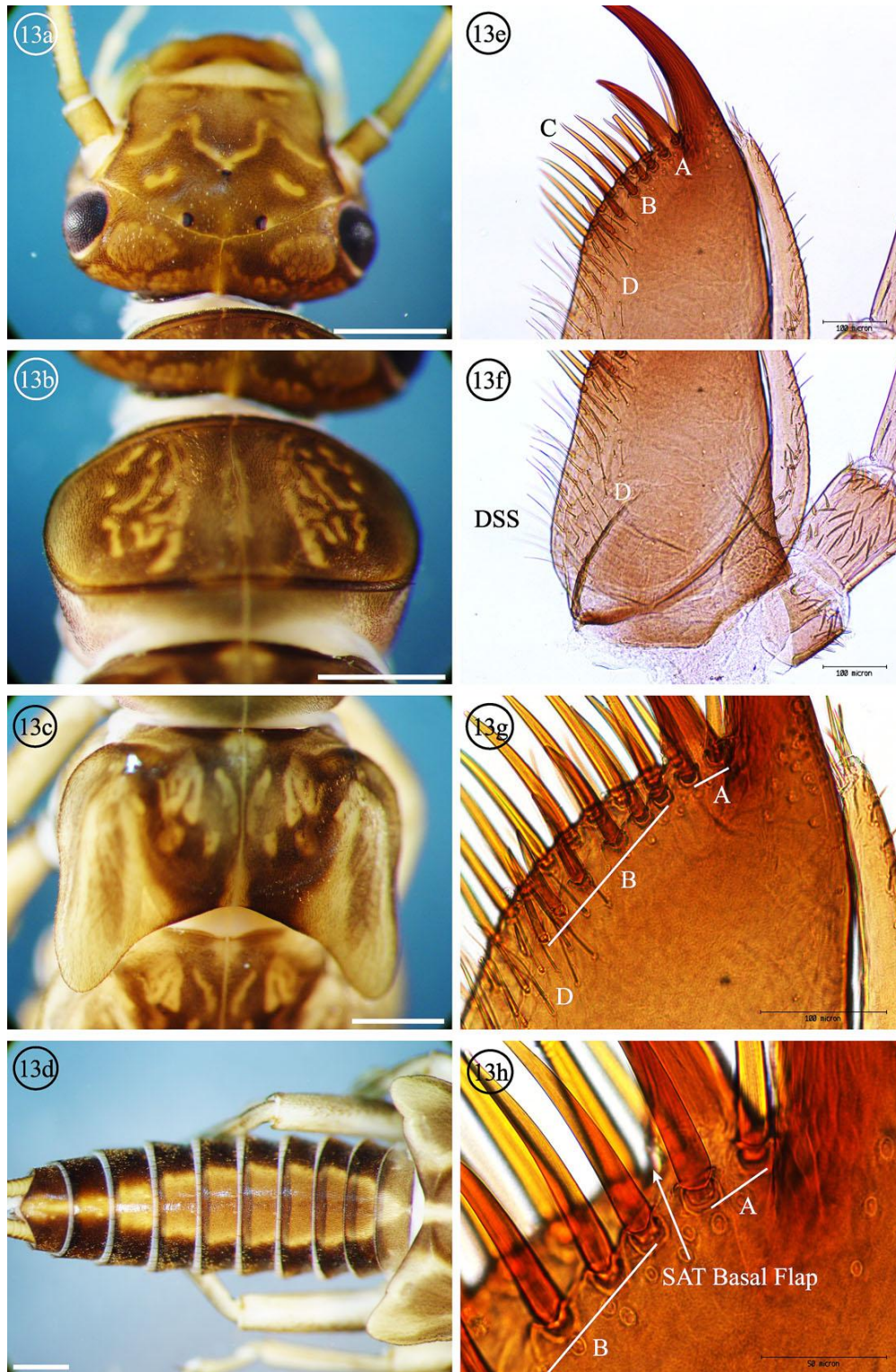
Isoperla muir Szczytko & Stewart
(Figs. 2k, 13a-h, 20k)

Isoperla muir Szczytko & Stewart 2004, 130:234-236. ♂, ♀, larva (reared), ovum.

Material examined. TYPE: *I. muir* Holotype ♂, OR: Douglas Co., Hwy 230, downstream from bridge, Muir Creek, 12/V/2002, S. Szczytko, K. Stewart (reared with exuviae) (NMNH); **Additional Specimens.** OREGON: Douglas Co., Muir Creek, Muir Camp, Hwy 230 bridge, 13.5 mi (21.7 km) E Hwy 138 intersection, 27/V/2008, 31/V/2008, J. Sandberg, Larvae (reared).

Male larva. Body length of mature larva 9–13 mm. **Dorsum of head** with contrasting pigment pattern and a mixture of fine light and dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus thin and well defined, not connected to light frontoclypeus area, median longitudinal light band absent, lateral thin arms directed posterolaterally, extending to antennal bases; posterior ocelli with completely enclosed small light areas along outer lateral margins; interocellar area entirely dark; occiput with irregular spinulae band extending from below eye to

near median epicranial suture, enclosed completely by dark pigment (Fig. 13a). **Lacinia** bidentate, total length 724–837 μm (Figs. 2k, 13e-h, Tables 2-4); submarginal row (A+B) with 7–9 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 13g); 2 submarginal setae (A) the first inserted at base of apical tooth (AT) inner margin, the second located between AT and SAT inner margins, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal seta (A), or broken, dorsal seta (DS) absent (Figs 13g-h); 5–7 submarginal setae (B) located past SAT inner margin (Fig. 13g); 9–11 marginal setae (C), initially long-stout and widely spaced, first marginal setae located under flap-like SAT inner margin (Fig. 13h – arrow), last few shorter and widely spaced (Fig. 13e); 33–58 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 13f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending at approximately the posterior-most ventral surface setae (Fig. 13f). **Galea** with 22–32 setae in sparse ventral row, apex with 5–6 setae. **Maxillary Palp** segments 2–3 with nearly straight, apically rounded setae. **Pronotum** with thin indistinct median light line bordered by irregular dark longitudinal bands with adjacent light rugosities; discs each with brown comma shaped lateral areas, fine dark clothing setae and lateral margins without broad light bands (Fig. 13b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 13c). **Legs** with numerous fine dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surfaces; fine silky setae absent on dorsal surface of femora, sparse on tibia (Fig. 20k); tibia with very faint transverse bands near proximal end. **Abdominal terga** with two distinct longitudinal dark stripes; wide light median longitudinal band widest on middle segments, narrowing anteriorly and posteriorly; lateral pair of dark longitudinal stripes extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with distinct and scattered long,



Figs. 13a-h. *Isoperla muir* nymph and ventral maxilla, Muir Creek, Douglas County, OR. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, and Dorsal surface setae DSS. White bars = 1 mm, 13e-f 100x, 13g 200x, and 13h 400x.

and numerous short spines in a concentrated row (Fig. 13d).

Distribution. Oregon, known only from the type location (Szczytko & Stewart 2004) where it occurs with *I. sobria*.

Diagnosis. The mature male larvae of *I. muir* are most similar to *I. adunca* in that the submarginal row (A+B) setae form a continuous and regularly spaced row (Figs. 13g-h). *Isoperla muir* can be separated from *I. adunca* by the submarginal setae row (A+B) regularly spaced at about the width of each seta base at points of insertion (Figs. 13a, g-h), dorsal seta (DS) absent and first marginal seta (C) covered by flap-like subapical tooth inner margin base (Fig. 13h).

Remarks. This distinctively pigmented species is rarely collected and is apparently restricted to the type locality. Limited rearing indicated emergence occurred in June.

Isoperla pinta Frison
(Figs. 2L, 14a-h, 20L)

Isoperla pinta Frison 1937, 21:92. Holotype ♂, Floras Creek, Curry Co., Oregon.

Isoperla pinta: Szczytko & Stewart 1979, 32:44-49. ♂, ♀, larva (not reared), ovum.

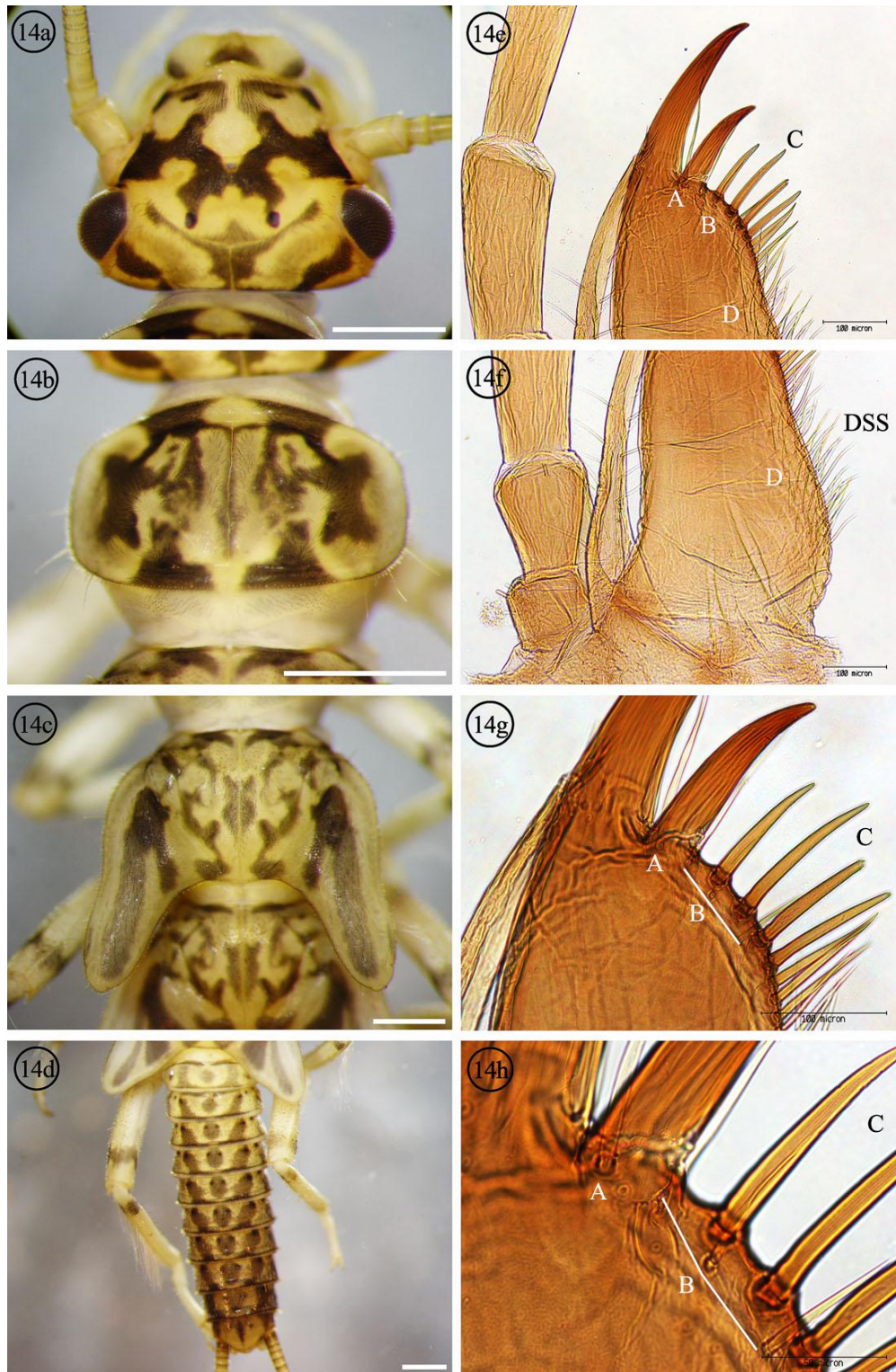
Material examined. CALIFORNIA: **Butte Co., Butte Creek**, Butte Creek Ecological Reserve, Honey Run Road, 2.9 mi (4.7 km) E intersection with Skyway, 13/I/2007, 05/II/2007, 11/IX/2007, J. Sandberg, Larvae; 17/II/2007, J. Sandberg, Larvae (reared), 04/III/2007, J. Sandberg, D. Pickard, ♂♀ Larvae (reared); 07/IV/2007, J. Sandberg, ♂♀; 18/I/2008, J. Sandberg, D. Pickard, Larvae; 04/II/2008, J. Sandberg, Larvae; 30/III/2008, ♂♀; 27/III/2009, ♂; 03/IV/2009, ♀; 19/II/2010, J. Sandberg, S. Hassur, Larvae (reared); 22/II/2010, J. Sandberg, Larvae (reared); 11/III/2010, J. Sandberg, J. York, Larvae (reared); 14/III/2010, J. Sandberg, Larvae (reared); 27/IV/2010, R. Baumann, B. Kondratieff, J. Sandberg, ♀; **El Dorado Co., Cosumnes River**, Michigan Bar, 18/IV/1986, R. Bottorff, ♂♀ (NMNH); **Humboldt Co., Mad River**, Arcata Bottoms, Mad River Road, N40.91578° W124.10618°, 10/IV/2010, J. Sandberg, ♂♀; **Monterey Co., ?**, Carmel, E. VanDuzee, 23/III/1919, ♂ relaxed in KOH (NMNH); **Plumas Co., Spanish Creek**, Hwy 70 bridge, Quincy Town Park, 10/III/2007, J.

Sandberg, Larva; **Sacramento Co., Cosumnes River**, Sloughhouse, 04/IV/1982, 25/V/1982, R. Bottorff, ♀ (NMNH); **Tulare Co., Lemon Creek**, Near Los Angeles, 14/IV/1950, R. Usinger, ♂♀ (NMNH); OREGON: **Benton Co., ?**, Corvallis, 06/IV/1907, J. Bridwell, ♂ (NMNH); **Clatsop Co., Nehalem River**, at Red Bluff Road 4 mi (6.4 km) NE Elsie, 17-18/IV/1965, S. Jewett Jr., ♀ (NMNH); **Curry Co., Rogue River**, Orchard Bar, Cty Hwy 595 (Agness Rd), 8.9 mi (14.3 km) NE Hwy 101, 14/II/2010, J. Sandberg, ♀, Exuviae; **Rogue River**, Coyote Bar, Cty Hwy 595 (Agness Rd), 5.6 mi (9.0 km) NE Hwy 101, 27/II/2010, J. Sandberg, Larvae; **Douglas Co., Cow Creek**, at Quines Creek, 08/IV/1968, S. Jewett Jr., ♀ (NMNH); **Josephine Co., Applegate River**, Location?, 23/II/1968, S. Jewett Jr., ♀ (NMNH); **Marion Co., Santiam River**, Near Jefferson, 11/IV/1967, S. Jewett Jr., ♀ (NMNH). **Santiam River**, Boat Launch & Rest Stop, I-5 bridge, 17 mi (27.3 km) S Salem, 19/III/2007, J. Sandberg, D. Pickard, J. Slusark, ♂.

Male larva. Body length of mature larva 10–13 mm.

Dorsum of head with contrasting pigment pattern and fine light and dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus not typical of western *Isoperla* species, usually connected to light frontoclypeus area by thin median longitudinal light band, lateral arms distinctly swollen at approximately mid length, usually directed laterally, extending to above antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area partially light, an irregular shape enclosed by dark brown pigment anteriorly and light brown pigment posteriorly; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 14a).

Lacinia bidentate, total length 682–841 μm (Figs. 2L, 14e-h, Tables 2-4); submarginal row (A+B) with 4–5 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Figs. 14g-h); 1–2 submarginal setae (A) the first inserted at base of apical tooth (AT) inner margin, the second when present, located between AT and SAT inner margins, first seta half as stout at base as marginal setae (C) and longitudinal striations weak or absent, all other species first seta nearly as stout and with striations, plus 1 thin marginal seta (TMS) adjacent to AT inner



Figs. 14a-h. *Isoperla pinta* nymph and ventral maxilla, Butte Creek, Butte County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, and Dorsal surface setae DSS. White bars = 1 mm, 14e-f 100x, 14g 200x, and 14h 400x.

margin, sometimes obstructed from view by AT or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or first submarginal setae (B) (Figs. 14g-h); 2–3 submarginal setae (B) located past SAT inner margin (Fig. 14h); 4–7 marginal setae (C), initially long-stout and widely spaced, last few shorter and variably spaced, blending into and difficult to differentiate from dorsal setae (Fig. 14e); 29–50 ventral surface setae (D) forming dense longitudinal band below marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, and concentrated in posterior half (Fig. 14f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 14f). **Galea** with 8–17 setae in sparse ventral row, apex with 4 setae. **Maxillary Palp** segments 2–3 with curved, apically rounded setae. **Pronotum** with irregular shaped median light area bordered by complex pattern of dark markings; discs each with distinctive lateral dark checkerboard pattern, fine dark and light clothing setae and lateral margins with broad light bands (Fig. 14b). **Meso and metanotum** with contrasting pigment pattern and fine dark and light clothing setae (Fig. 14c). **Legs** with numerous light and dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surface; fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20L); distal femur and proximal tibia with transverse bands. **Abdominal terga** with three distinct longitudinal stripes and small dark spots arranged in pairs on dorsal surface and in triplets laterally; wide light median longitudinal band bisected with irregular shaped dark median stripe; lateral pair of dark longitudinal stripes about as wide as median dark stripe, not extending to lateral margins; numerous fine light clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 14d).

Distribution. Canada: British Columbia, Alberta; USA: California, Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming. Mexico: Baja California. Widely distributed throughout northern California.

Diagnosis. The male larvae of *I. pinta* are distinct among other western *Isoperla* species with 2–4 submarginal setae (A+B). The 1–2 submarginal setae (A) are less than half as stout at their base than the largest marginal setae (C) and lack or possess weak longitudinal striations (Figs. 14g-h).

Remarks. The distinctive head and pronotal pigment pattern of larvae could be used alone to identify individuals of this species in California, where *Isoperla phalerata* Needham has not been collected. In Butte Creek, Butte County, it was the first of three *Isoperla* species to emerge in March–April.

Specimens examined in this study were compared with *I. phalerata* from previous drumming studies (Sandberg 2011, Sandberg & Stewart 2006), and the adults, larvae and drumming characters could not be separated. Perhaps these are sibling species and can only be separated by very slight aedeagus character differences or Scanning Electron Microscope characters of the ovum (Szczytko & Stewart 1979 – Figs. 64-71). However, it seems likely the Colorado *I. phalerata* population studied in Sandberg & Stewart (2006) was actually *I. pinta*. Further study is needed to confirm the identity of these two very closely related species.

Isoperla quinquepunctata (Banks)
(Figs. 2m, 15a-h, 20m)

Chloroperla quinquepunctata Banks 1902, 34:124. Holotype ♀.

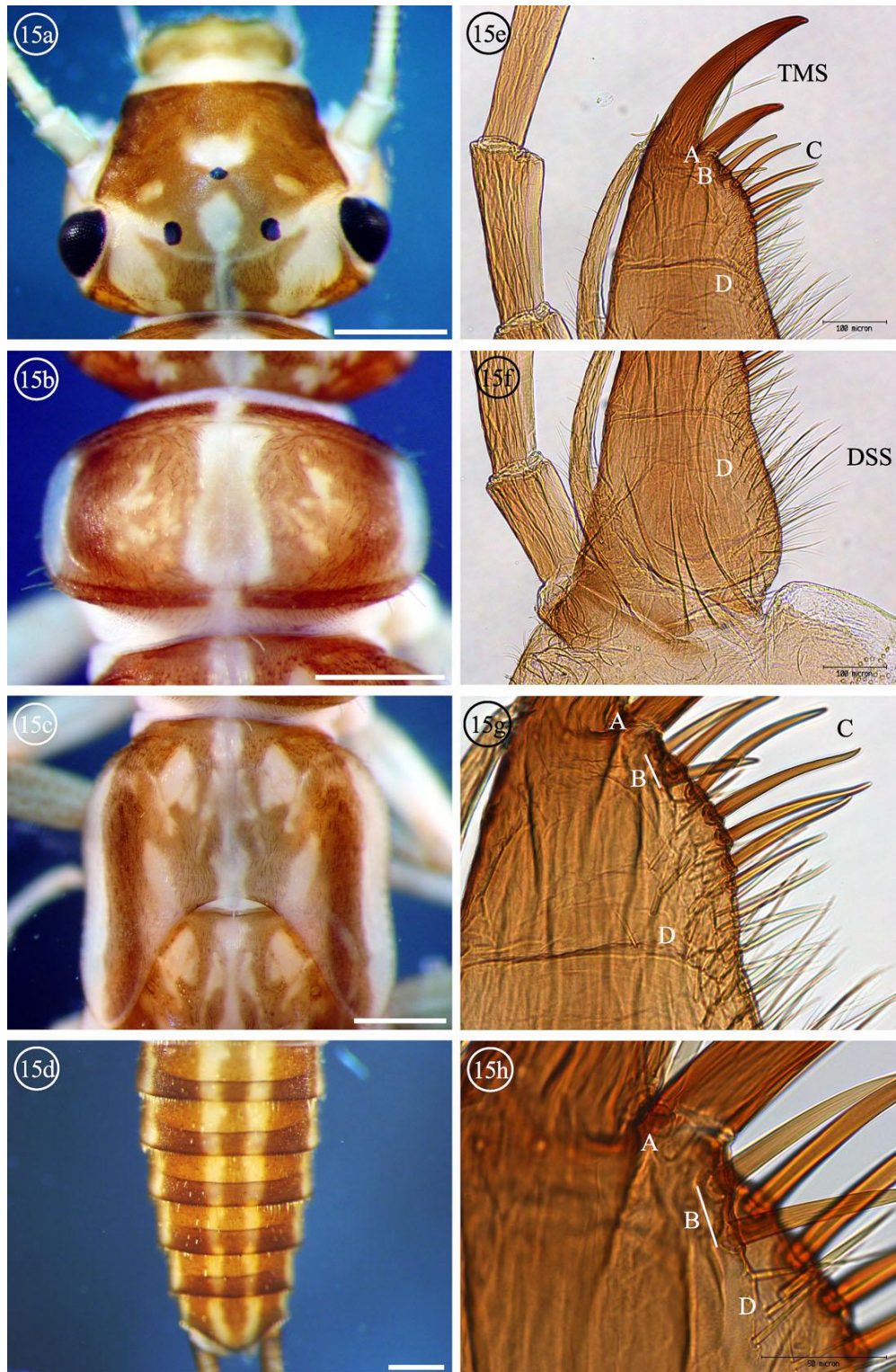
Isoperla quinquepunctata: Szczytko & Stewart 1979, 32:27-36. ♂, ♀, larva (reared), ovum.

Material examined. CALIFORNIA: **Butte Co., Butte Creek**, Butte Creek Ecological Reserve, Honey Run Road, 2.9 mi (4.7 km) E intersection with Skyway, 07/IV/2007, J. Sandberg, ♂; 11/V/2007, J. Sandberg, S. Hassur, ♂, Larvae; 03/IV/2009, J. Sandberg, Larvae; 14/III/2010, J. Sandberg, Larvae; 27/IV/2010, R. Baumann, B. Kondratieff, J. Sandberg, ♂; **Butte Creek**, Hwy 99 bridge, Chico, 11/V/2007, J. Sandberg, S. Hassur, ♀; **El Dorado Co., NF Cosumnes River**, Sweeney's, Somerset, 13-21/VI/1982, R. Bottorff, ♀ (NMNH); **NF Cosumnes River**, Hwy 49, Nashville, 01/VI/1981, R. Bottorff, ♀ (NMNH); **Napa Co., Capell Creek**, 2.1 mi (3.4 km) W Rt 121 on Rt 128, 20/VI/1985, O. Flint, ♂♀ (NMNH); **Placer Co.,**

Truckee River, Rt 89, 9 mi (14.5 km) S I-80, 5000 feet (1524m), 19/VI/1985, C. & O. Flint, ♂♀ (NMNH); **Sacramento Co.**, Cosumnes River, Michigan Bar, 23/IV/1982, 30/IV/1982, 06/VII/1982, 30/III/1984, 29/IV/1986, R. Bottorff, ♂♀ (NMNH); Cosumnes River, Sloughhouse, 04/IV/1982, 13/V/1982, 25/V/1982, 14/VI/1982, R. Bottorff, ♂♀ (NMNH); **Tehama Co.**, Sacramento River, Near Red Bluff, 31/III/1965, S. Jewett Jr., ♂ (NMNH); **Tulare Co.**, Kaweah River?, Near Three Rivers, 14/V/1964, D. Denning, ♂♀ (NMNH); **Yuba Co.**, Yuba River, Hammon Grove Park, Hwy 22, 13 mi (20.9 km) NE Marysville, 07/V/2010, J. Sandberg, ♂♀, Larvae (reared); Yuba River, Hwy 22 bridge crossing, 16.4 mi (26.4 km) NE Marysville, 02/V/2010, J. Sandberg, A. Richards, ♂♀, Larvae (reared); 07/V/2010, J. Sandberg, ♂♀, Larvae (reared); OREGON: **Baker Co.**, ?, Sumpter, on willow, 19/VII/1971, J. Baker, ♂ (NMNH); **Clatsop Co.**, Nehalem River, at Red Bluff Rd., 4 mi (6.4 km) NE Elsie, 08/V/1965, S. Jewett Jr., ♀ (NMNH); **Grant Co.**, ?, Ritter, 18/VII/1962, Clarke, ♂♀ (NMNH); **Klamath Co?**, ?, Odell Lake, Cascade Mts, 4760 feet (1451m), 16/VII/1948, C. Alexander, ♂♀ (NMNH).

Male larva. Body length of mature larva 9–12 mm. **Dorsum of head** with contrasting pigment pattern and a mixture of fine light and dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus usually indistinct, not connected to light frontoclypeus area, median light longitudinal light band absent, lateral thin arms faint, directed posterolaterally, extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area partially light and variable, either completely enclosed by dark pigment and entirely within the triangle, enclosed by dark pigment and extended posteromedially past posterior ocelli, or connected to posterior margin of head by thin longitudinal light pigment band; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 15a). **Lacinia** bidentate, total length 696–828 μm (Figs. 2m, 15e-h, Tables 2-4); submarginal row (A+B) with 3–4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Figs. 15g-h); 1 submarginal seta (A) inserted at the base apical tooth (AT) inner

margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT (Figs. 15g-h); 2–3 submarginal setae (B) located past SAT inner margin (Fig. 15h); 7–11 marginal setae (C), initially long-stout and widely spaced, last few shorter and widely spaced, blending into and difficult to differentiate from dorsal and ventral surface setae (Fig. 15e); 48–97 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 15f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 15f). **Galea** with 23–27 setae in sparse ventral row, apex with 5 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area occasionally with a short central indistinct brown band bordered by irregular dark pigment markings; discs each with partially to completely enclosed light areas, the largest resembling the “windows” described for *I. acula*, fine dark clothing setae and lateral margins with broad light bands (Fig. 15b). **Meso and metanotum** with contrasting pigment pattern and fine light and dark clothing setae, dark setae enclosed by dark pigment (Fig. 15c). **Legs** with numerous fine light clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surfaces; fine silky setae numerous and continuous on dorsal surfaces of femora and tibia (Fig. 20m); tibia with at most, a very faint and incomplete band near joint with femora; femora with median, longitudinal light brown pigment band concentrated distally. **Abdominal terga** with three distinct longitudinal dark stripes; wide light median longitudinal band bisected with variable, thin to thick, dark median longitudinal stripe; lateral pair of dark longitudinal stripes about twice as wide as median dark stripe, nearly extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 15d).



Figs. 15a-h. *Isoperla quinquepunctata* nymph and ventral maxilla, Butte Creek, Butte County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae, and Thin marginal setae TMS. White bars = 1 mm, 15e-f 100x, 15g 200x, and 15h 400x.

Distribution. Canada: Alberta, British Columbia and Saskatchewan; USA: California, Colorado, Idaho, Kansas, Montana, Nebraska, New Mexico, Nevada, Oregon, South Dakota, Utah, and Wyoming; Mexico: Baja California. Widely distributed throughout California.

Diagnosis. Mature male *I. quinquepunctata* larval pigment patterns are most similar to *I. acula*, *I. mormona* and *I. sordida* (Figs. 3a-d, 12a-d, 15a-d, 18a-d). In California, this species can be differentiated from other species with 1–4 submarginal setae (A+B) by having 48–97 ventral surface (D) setae (Figs. 15e-h), pronotal discs patterned with small to large central light areas, when large these areas not completely enclosed by dark pigment (Fig. 15b).

Remarks. When live, larvae of this species possess a distinctive red hue on non-sclerotized membrane. This species was found in large creeks and medium rivers with fast currents and with one or more of the following species: *I. pinta*, *I. mormona*, *I. marmorata*, and *I. roguensis*. Emergence occurred in May–June.

Isoperla roguensis Szczytko & Stewart
(Figs. 2n, 16a-h, 20n)

Isoperla roguensis Szczytko & Stewart 1984, 77:260-262.
♂, ♀, ovum.

Isoperla roguensis: Szczytko & Stewart 2002, 128:2-3.
Larva (not reared).

Isoperla karuk Baumann & Lee 2009, 5:5-9. ♂, ♀, ovum.
NEW SYNONOMY.

Material examined. TYPES: *I. roguensis*, Holotype ♂, Allotype ♀, OR: **Curry Co.**, Mouth of the Rogue River, 30/III/1949, S. Jewett Jr. (NMNH #10469). Paratype ♂ (2 of 3 cleared with KOH), same as Holotype (Stan Szczytko Collection – University of Wisconsin-Stevens Point). **Additional Specimens.** CALIFORNIA: **Butte Co.**, Butte Creek, Butte Creek Ecological Preserve, Honey Run Road, 2.9 mi (4.7 km) E of intersection with Skyway, 13/I/2007, 05/II/2007, J. Sandberg, Larvae; 04/III/2007, J. Sandberg, D. Pickard, Larvae (reared); 07/IV/2007, J. Sandberg, ♂♀, Larvae (reared); 13/IV/2007, J. Sandberg, ♂♀; 18/I/2008, J. Sandberg, D. Pickard, Larvae; 30/III/2008, J. Sandberg, ♂♀, Larvae; 30/IV/2008, J. Sandberg, ♀; 27/III/2009, J. Sandberg, Larvae; 03/IV/2009, J. Sandberg, ♂♀; 19/II/2010, J.

Sandberg, S. Hassur, Larvae; 22/II/2010, J. Sandberg, Larvae (reared); 11/III/2010, J. Sandberg, J. York, Larvae (reared); 14/III/2010, J. Sandberg, Larvae (reared); Big Chico Creek, Big Chico Creek Ecological Reserve, N39.86909°, W121.70760°, near north boundary, 27/IV/2010, R. Baumann, B. Kondratieff, J. Sandberg, ♀; Big Chico Creek, Five-Mile Recreation Area, Centennial Ave & Crow Canyon Ct, Chico, 27/III/2010, J. Sandberg, ♂♀, Larvae (reared); **Humboldt Co.**, Klamath River, Aikens Creek Campground, Hwy 96, 4.7 mi (7.6 km) NE Weitchpec, 09/IV/2010, J. Sandberg, ♂♀, exuviae; Mad River, Arcata Bottoms, Mad River Road, N40.91578°, W124.10618°, 10/IV/2010, J. Sandberg, ♂♀; **Plumas Co.**, Spanish Creek, Spanish Creek Campground, 3 mi (4.8 km) N Keddie, 04/III/2007, J. Sandberg, D. Pickard, Larvae (reared); **Tehama Co.**, Mill Creek, 1000 ft (305 m) upstream of Sacramento River confluence, Elev. 208 ft (63.4 m), 13/IV/2011, J. Dittes. OREGON: **Curry Co.**, Rogue River, Orchard Bar, Cty Hwy 595 (Agness Road), 8.9 mi (14.3 km) NE Hwy 101, J. Sandberg, Larvae (reared); 20/III/2010, J. Sandberg, ♀, Larvae (reared); Rogue River, Rotary Riverside Trail, Cty Hwy 595 (Jerry's Flat Road), 0.35 mi (0.6 km) NE Hwy 101, 21/III/2010, J. Sandberg, ♀.

Male larva. Body length of mature larva 9–12 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus variable, usually indistinct, not connected to light frontoclypeus area and completely enclosed in dark pigment, median longitudinal light band absent, lateral thin arms faint, lacking clothing setae, directed posterolaterally and extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; interocellar area variable, from completely dark to partially light, when small light area present, completely enclosed by dark pigment and not extending posteriorly past posterior ocelli; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 16a). **Lacinia** bidentate, total length 682–862 μm (Figs. 2n, 16e-h, Tables 2-4); submarginal row (A+B) with 3 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 16g); 1 submarginal seta (A)

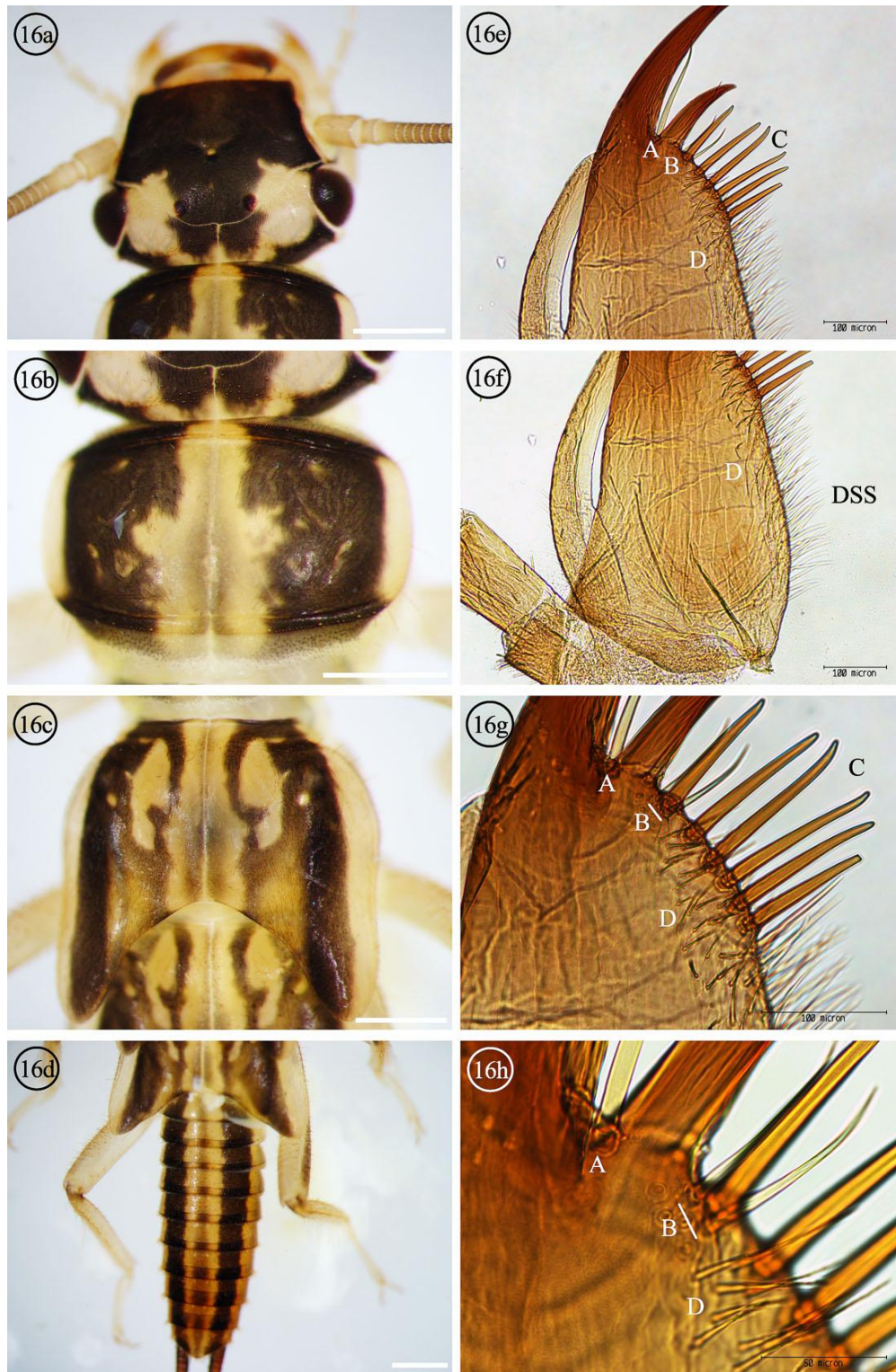
inserted at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal seta (A) or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 16g-h); 2 submarginal setae (B) located past SAT inner margin (Fig. 16h); 5–9 marginal setae (C), initially long-stout and widely spaced, last few shorter and widely spaced, blending into and difficult to differentiate from dorsal and ventral surface setae (Fig. 16e); 48–88 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 16f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 16f). **Galea** with 19–27 setae in sparse ventral row, apex with 4–6 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with median light area occasionally with a thin central indistinct brown band bordered by wide dark irregular pigment bands typical of the *I. marmorata* group; discs each with variable and irregular inner lateral dark pigment margins, variable light rugosities usually concentrated along inner dark band margins, fine dark clothing setae except over rugosities and lateral margins with broad light bands (Fig. 16b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 16c). **Legs** with numerous fine golden to light brown clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surface; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20n); tibia with extremely faint transverse bands near proximal end. **Abdominal terga** variable, usually with two distinct longitudinal dark stripes; wide light median longitudinal band sometimes bisected by faint, light brown longitudinal median band; lateral pair of dark longitudinal stripes usually not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 16d).

Distribution. California, Oregon. Widely distributed in northern California.

Diagnosis. Mature male larvae of *I. roguensis* are most similar to *I. fulva* and *I. marmorata*. The larvae of this species can not be separated from *I. fulva* but can be distinguished from *I. marmorata* by the lack of or reduced M shaped light pattern not connected to unpigmented frontoclypeus (Fig. 16a). Pigment patterns are known to vary in *Isoperla* and a non-pigment character must be found before increased species resolution can be achieved in the *I. marmorata* complex.

Remarks. The three western species included in the *I. marmorata* complex have similar dark larval pigment patterns. In several locations, *I. roguensis* was found with one or more of the following: *I. marmorata*, *I. mormona*, *I. pinta* or *I. quinquepunctata*. Emergence was slightly extended and occurred in March–May.

Isoperla karuk is placed as a new junior subjective synonym of *I. roguensis* based upon comparison with reared material from the type localities, additional California locations and comparison of the aedeagii with the everted and cleared *I. roguensis* paratypes held in the collection of Dr. Stanley Szczytko, University of Wisconsin-Stevens Point. The authors of *I. karuk* (Richard Baumann, Per. com) based their description upon an everted aedeagus of a live adult (Bauman & Lee 2009 - Figs. 17-24) which seemed different from the hyper everted and cleared aedeagus of an already preserved adult in Szczytko & Stewart (1984 - Fig. 55). An important consideration for future adult taxonomy of this genus is that no two live adult males can be everted to the same extent. The adult male aedeagus is a thin membranous inverted sac, that when squeezed out of the posterior ninth sternal inter-segmental membrane (eversion), is filled with seminal fluid (like a balloon). The consistent eversion of lobes and placement of diagnostic setae patches or sclerotized posterior processes are confounded by 1) the amount and length of time of eversion (should take place under a dissecting microscope to ensure full eversion) and 2) whether the aedeagus was fixed in near boiling water. If less eversion pressure or no hot water fixation was used, the aedeagus will invert to some degree. The comparison of live everted versus preserved hyper everted males is further complicated by the clearing method used in Szczytko & Stewart



Figs. 16a-h. *Isoperla roguensis* nymph and ventral maxilla, Butte Creek, Butte County, CA. Submarginal setae A and B, Marginal setae C, Ventral surface setae D, and Dorsal surface setae DSS. White bars = 1 mm, 16e-f 100x, 16g 200x, and 16h 400x.

(1979), which presumably allows internal lobes and lobe-like structures to become everted (See *I. baumannii*).

Isoperla sobria Hagen
(Figs. 2o, 17a-h, 20o)

Isoperla sobria Hagen 1874, 7:577. Holotype ♀.

Perla ebria Hagen 1874, 7:577. Holotype ♀.

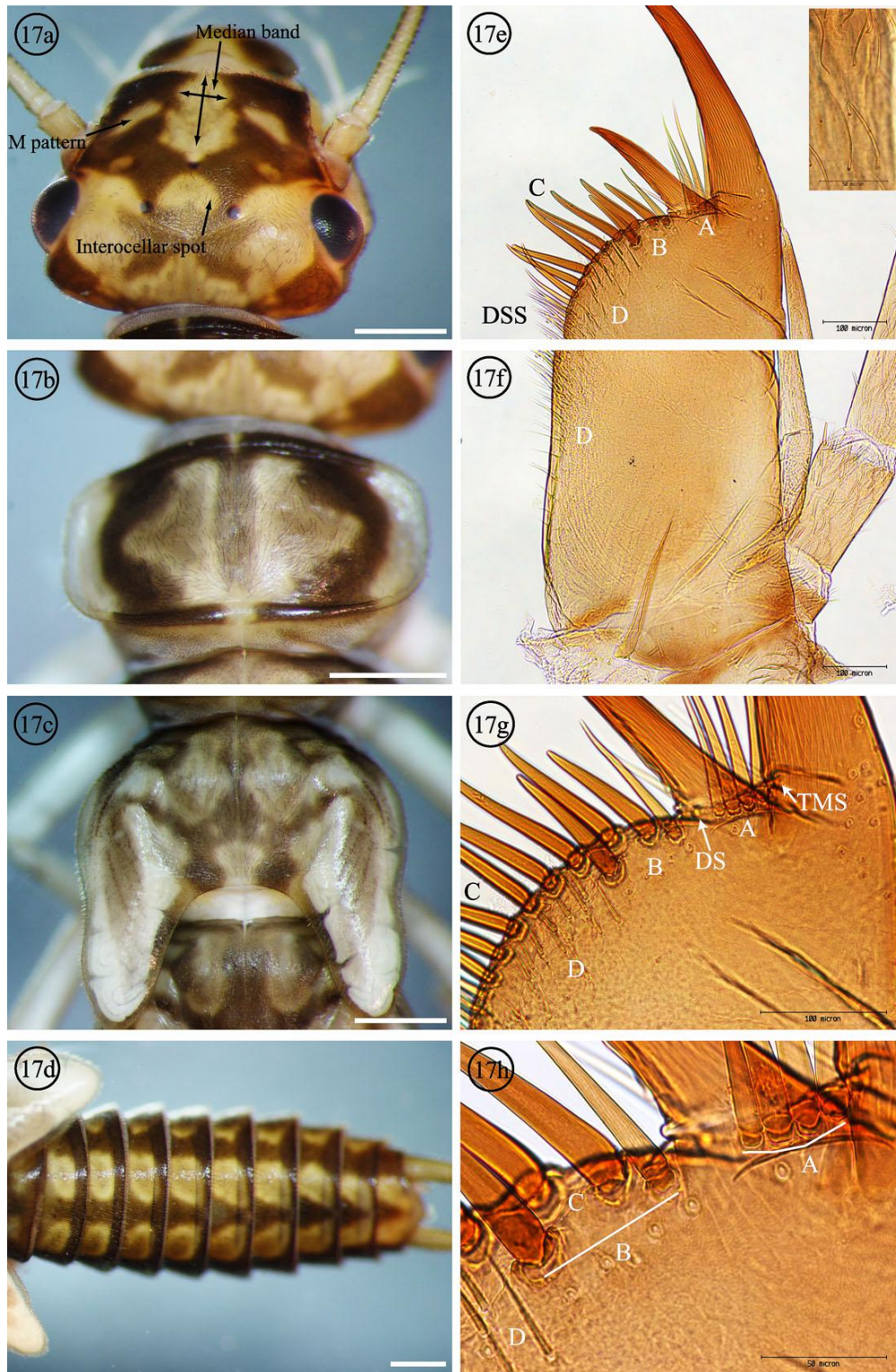
Isoperla sobria: Szczytko & Stewart 1979, 32:49-56. ♂, ♀, larva (reared), ovum.

Material examined. ALASKA: **Matanuska - Susitna Border**, Montana Creek, Hwy 3 bridge near Montana, 08/VI/2006, J. Sandberg, J. Harrington, D. Pickard, J. Slusark, T. Morman, Female Exuviae; CALIFORNIA: **Butte Co.**, Butte Creek, Cherry Hill Campground (Humboldt Rd) 9 mi (14.5 km) NE Lomo (Hwy 32), 06/I/2007, J. Sandberg, A. Richards, Larvae; 27/I/2007, J. Sandberg, Larva; 03/II/2007, J. Sandberg, A. Richards, Larva; 01/IV/2007, J. Sandberg, Larva; 20/III/2008, J. Sandberg, S. Sandberg, Larvae; 26/IV/2010, R. Baumann, B. Kondratieff, A. Richards, J. Sandberg, J. Slusark, ♂ (reared); Butte Creek, Humboldt Road bridge at Colby/Willow Creeks, 0.25 mi (0.4 km) W Jonesville, 25/V/2008, J. Sandberg, ♂; **Colusa Co.**, Big Springs tributary, Big Springs Picnic Area, Letts Lake, FR 17N02, Mendocino NF, 03/II/2009, J. Sandberg, D. Pickard, Larvae; Lily Pond unmapped outflow, W Lily Pond FR 17N02 crossing, Mendocino NF, 03/II/2009, J. Sandberg, D. Pickard, Larvae; Little Stony Creek, FR 18N07, 20 mi SW Stonyford, Mendocino NF, 01/II/2009, J. Sandberg, A. Richards, Larvae; **Contra Costa Co.**, ?, Martinez, ?/VI/1910, J. Grundell, ♂ cleared (NMNH); **El Dorado Co.**, Tributary of NF Cosumnes River, above Meiss Ranch, 06/VI/1986, R. Bottorff, Female Larvae, Male Exuviae (mounted lacinia slide # 015) (NMNH); Rubicon River, ?location, 05/IX/1954, S. Hitchcock, Larvae (NMNH); **Mariposa Co.**, Tamarack Creek, Yosemite National Park, 6300 feet, 30/V/1955, S. Hitchcock, Larvae (mounted lacinia slide #014) (NMNH); **Nevada Co.**, ?spring, entering Sagehen Creek, 6400 feet, 05/VI/1965, A. Sheldon, Male Larvae (mounted lacinia slide #013) (NMNH); Spring head of Hanging Bog, Sagehen Creek, 6300 feet, 23/V/1966, ♂, 13/IX/1965, A. Sheldon, ♂♀ (NMNH); Bog Spring, Sagehen Creek, 22/VI/1966, ♀; 07/VII/1966, A.

Sheldon, ♂ (NMNH); Spring Trib, to Sagehen Creek, 30/VI/1965, ♂; 01/VIII/1965, ♂; 11/VIII/1965, ♂♀; 26/VIII/1965, ♀; 31/VIII/1965, ♂♀; 13/IX/1965, A. Sheldon, ♂♀ (NMNH); Sagehen Creek, Sagehen Creek Project, Spring Run, 6400 feet, 02/VI/1965, A. Sheldon, Female larvae (mounted lacinia slide #0102) (NMNH); Sagehen Creek, 6400 feet, 05/VI/1965, Larvae; 24/VI/1965, A. Sheldon, ♂♀ (NMNH); Sagehen Creek, 6300 feet, 30/V/1965, ♀; 01/VI/1966, A. Sheldon, ♀ (NMNH); Sagehen Creek, Diversion, 02/VI/1966, ♂; 09/VI/1966, ♂; 11/VII/1966, A. Sheldon, ♀ (NMNH); Sagehen Creek, Station Spring, 25/VII/1966, A. Sheldon, ♂ (NMNH); Sagehen Creek, ?location, 19/VI/1985, O. Flint, ♀, Larvae; **Placer Co?**, ?, on Carnelian Bay, Lake Tahoe, 24/VI/1954, S. Hitchcock, ♂♀ (NMNH); **Plumas Co.**, Big Grizzly Creek, 0.4 mi (0.6 km) S Beckwourth Rd on Unnamed Rd, 6 mi (9.6 km) E Lake Davis, 30/VI/2006, ♀ (Malaise Trap); 15/XII/2006, J. Sandberg, A. Richards, Larvae; Cow Creek, 2 mi (3.2 km) NE Smith Peak nr intersection with jeep trail, 21/VI/2006, larvae; 30/VI/2006, J. Sandberg, A. Richards, ♀ (Malaise Trap); Freeman Creek, 2 mi (3.21 km) S on Threemile Valley Rd, S Lake Davis, 21/VI/2006, Exuviae; 30/VI/2006, ♂♀ (Malaise Trap), J. Sandberg, A. Richards; Mosquito Creek (West Branch), 0.4 mi (0.6 km) E Domingo Springs, 8.1 mi (13.0 km) W of Chester, 04/II/2007, J. Sandberg, Larvae; 22/IV/2007, J. Sandberg, D. Pickard, Larvae (reared); 19/V/2007, J. Sandberg, S. Hassur, ♀, Larvae (reared); 28/V/2007, J. Sandberg, D. Pickard, ♀, Larvae (reared); 13/VI/2007, J. Sandberg, Larvae (reared); 16/IX/2007, J. Sandberg, Larvae; 03/XI/2007, J. Sandberg, Larvae; 17/V/2008, J. Sandberg, Larvae; 13/VI/2008, J. Sandberg, ♂♀, Larvae (reared); 20/VI/2008, J. Sandberg, ♂, Larvae (reared); 05/VI/2010, J. Sandberg, Larvae (reared); 03/VII/2010, J. Sandberg, ♂♀, Larvae (reared); Spring Trib of Lake Davis (Corral), Feeding SE Lake Davis on Threemile Valley Rd, 29/V/2006, J. Sandberg, D. Pickard, J. Slusark, Larvae (reared); 27/X/2006, J. Sandberg, A. Richards, Larvae; 06/VI/2010, J. Sandberg, J. Slusark, Larvae (reared); 04/VII/2010, J. Sandberg, ♂♀, Larvae (reared); Spring Trib of Lake Davis (Moselia), Feeding E Lake Davis, 0.5 mi (0.8 km) E Freeman Cr, 29/V/2006, J. Sandberg, D. Pickard, J. Slusark, ♀, Larvae; 21/VI/2006, J. Sandberg, A. Richards, Larvae; **Sierra Co.**, Weber Lake, Little Truckee River?, Henness Pass Road,

04/VII/1965, P. Arnaud, ♀ (CAS); **Shasta Co.**, ?, Burney Falls, 17/IX/1946, H. Chandler, ♀ (CAS); **NE Battle Creek**, ?location, 04/VII/1953, H. Chandler, ♀ (CAS); **Tehama Co.**, **Gurnsey Creek**, Gurnsey Creek Campground, Hwy 36 (89), 2.3 mi (3.7 km) N Hwy 32 intersection, 27/I/2007, J. Sandberg, Larva; **Tulare Co.**, ?, Sequoia National Park, Giant Forest, 6400 feet, 19/VI/1963, C. Alexander, ♀ (NMNH); **Tuolumne CO.**, **Gaylor Lakes**, Yosemite NP East, 1000 feet, 08/VII/1945, H. Chandler, ♀ (CAS); COLORADO: ?**County**, ?River, Longs Peak, 12/VII/1926, E. Vandyke, ♂♀ (CAS); IDAHO: **Franklin Co.**, ?, Willow Flat Forest Camp, Cub River Canyon, Wasatch Mts, 4-5/VII/1952, B. Malkin, ♂ (CAS); OREGON: **Baker Co.**, **Pine Creek**, ?location, 26/VI/1948, J. Baker, ♀ (CAS); **Benton Co.**, **Oak Creek**, Corvallis, 02/IV/1935, R. Dimick, ♂ cleared (NMNH); **Oak Creek**, 6.75 mi (10.9 km) NW Corvallis, Rt branch Oak Cr., E Patterson Rd., 1.5 mi (2.4 km) N of Fish lab, 700 feet, 16-19/V/1969, C. Kerst, ♂ (NMNH); 16-19/V/1969, C. Kerst, ♂ damaged (NMNH); **Clackamas Co.**, **Still Creek**, Swim Cr., 15/VI/1947, S. Jewett Jr., ♀ (CAS); **Coos Co.**, **Wooden Rock Creek**, Pioneer Campground, NFD 240 Rd, 0.2 mi (0.3 km) N NFD 3348 Rd intersection, 19/III/2010, J. Sandberg, Larvae; **Deschutes Co.**, **Fall River**, ?location, 13/VII/1948, S. Jewett Jr., ♂♀ (CAS); **Fall River**, Fall River Campground, Hwy 42 (S Century Dr), 13 mi (20.9 km) E Hwy 97, 28/V/2008, 31/V/2008, J. Sandberg, ♂♀, Exuviae, Larvae (reared); **Douglas Co.**, **Muir Creek**, Muir Camp, Hwy 230 bridge, 13.5 mi (21.7 km) E Hwy 138 intersection, 27/V/2008, 31/V/2008, Larvae (reared); **Grant Co?**, **Lunch Creek**, Blue Mountains, 24/VI/1952, B. Malkin, ♀ (CAS); **Hood River Co.?**, ?, Hood River Meadows, Mt Hood, 18/VII/1947, K. Fender, ♀ (CAS); ?River, Hood River Meadows, E side of Hood, 4475 feet, 31/VII/1948, C. Alexander, ♀ (NMNH); **Klamath Co.**, **Spring Creek**, Collier State Park, Hwy 97, 3.7 mi (5.9 km) N Pine Ridge, 12/V/1950, S. Jewett Jr., ♂♀ (CAS); **Linn Co.**, **Marion Creek**, Marion Creek (Lake) Rd at Willis Creek confluence, 08/VI/2011, J. Sandberg, ♂ Exuviae; WASHINGTON: **Cowlitz Co.**, **Upper Kalama River**, ?location, 01/XII/1966, O. Flint, ♂ (NMNH); **Pierce Co?**, **Nisqually River**, Mt Rainier NP, 13/VII/1936, E. Vandyke, ♀ (CAS); **Skamania Co.** **Tyee Spring**, Meadow Creek Rd, 0.44 mi (0.71 km) N NFD 3065 &

NFD 30 Rds, 16/VI/2011, J. Sandberg, ♂♀ Exuviae. **Male larva.** **Body** length of mature larva 10–13 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus connected to light frontoclypeus area by a median longitudinal light band, its width approximately equal to the posteromedian portion of the light M shaped pattern, lateral arms with irregular margins usually disconnected from median light area, directed posterolaterally, and extending to antennal bases; posterior ocelli with partially enclosed large light areas along outer lateral margins; intercellular area variable, usually partially light and shaped like an inverted V, completely enclosed by dark pigment and not extending past posterior ocelli, sometimes a small spot; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 17a). **Lacinia** bidentate, total length 901–1265 µm (Figs. 2o, 17e-h, Tables 2-4); submarginal row (A+B) with 5–6 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 17g); 3–4 submarginal setae (A) in a close set row beginning at base of apical tooth (AT), ending before reaching SAT inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal setae (A), or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT; 2 submarginal setae (B) located past SAT inner margin (Figs. 17g-h); 10–17 marginal setae (C), initially long-stout and widely spaced, sometimes several setae near end of row arranged in pairs protruding at dorsal and ventral angles, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 17e); 21–58 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, occasionally a few setae located below submarginal row striated (Fig. 17f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band, concentrated at junction with marginal setae (C), ending at approximately $\frac{1}{2}$ or a little more the lacinia length (Fig. 17e). **Galea** with 12–23 setae in sparse ventral row, apex with 2 setae. **Maxillary Palp** segments 2–3



Figs. 17a-h. *Isoperla sobria* nymph Fall River, Deschutes County, OR and ventral maxilla, Mosquito Spring Creek, Plumas County, CA. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal surface setae, Dorsal seta DS, and Thin marginal seta TMS. White bars = 1 mm, 17e-f 100x, 17g 200x, and 17h 400x.

with curved, apically pointed setae (Inset, Fig. 17e). **Pronotum** with large median light area bordered thick dark comma shaped bands typical of the *I. sobria* complex, a range of irregular shaped faded light brown areas usually present between the dark commas and entirely covered by fine dark clothing setae, lateral margins with broad light bands (Fig. 17b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 17c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20o); distal femora and proximal tibia with distinct transverse bands. **Abdominal terga** with three distinct longitudinal dark stripes; wide light median band bisected with irregular shaped, dark median longitudinal stripe; lateral pair of dark longitudinal stripes about twice as wide as median dark stripe, usually not extending to lateral margins; numerous fine light clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 17d).

Distribution. Canada: Alberta, British Columbia and Yukon territory; USA: Alaska, Arizona, California, Colorado, Idaho, Montana, New Mexico, Nevada, Oregon, Utah, Washington, and Wyoming. In northern California, widely distributed at higher elevations.

Diagnosis. Mature male larvae of *I. sobria* are distinctive with the following characters: the lacinia submarginal row (A) has 3–4 close set setae (Figs. 17e, g-h), the completely enclosed inverted V shaped interocellar light area does not extend past posterior ocelli (Fig. 17a), and basal segments 2–3 of the maxillary palpi have long, thin apically pointed setae (Fig. 17a Inset). The interocellar light area was sometimes only a very small spot. It shares a similar dark comma shaped pronotal pigment pattern with the other species in the *I. sobria* complex (Figs. 5b, 11b, 17b, 19b). Only *I. miwok* lacked the multiple submarginal setae (A) character (Figs. 11e, g-h).

Remarks. The abdominal pigment stripes of some male and female larvae faded quickly in ethanol and the abdomen became completely dark, losing the light longitudinal stripes. Emergence was slightly

extended and occurred in May–July. Adult females had slightly longer subgenital plates than what is illustrated (Fig. 89, Szczytko & Stewart 1979). The typical *I. sobria* subgenital plate had nearly parallel lateral margins, extended posteriorly to nearly the mid length of abdominal sternite nine, and the apical margin was broadly rounded.

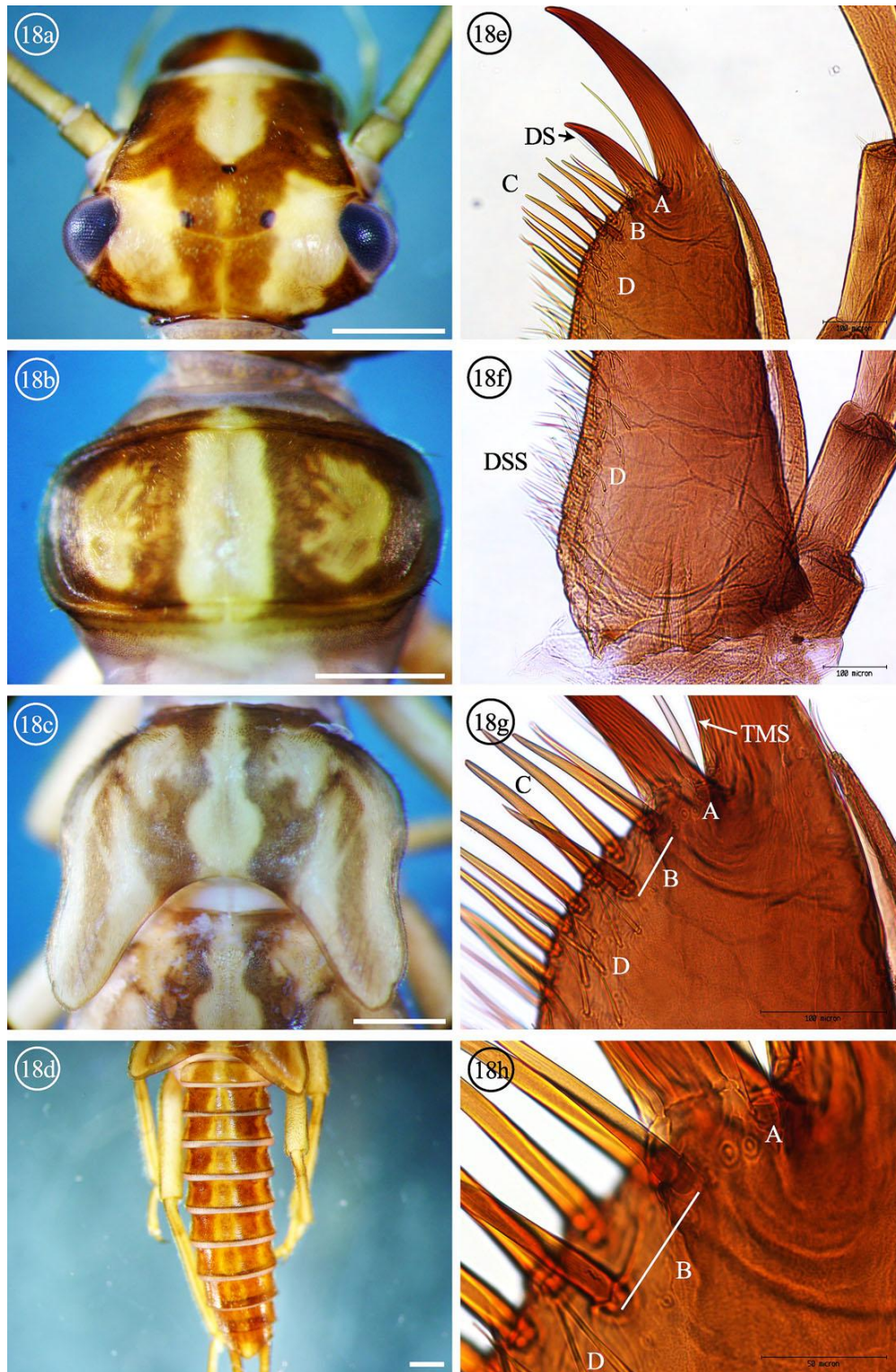
There were observations which may extend the ranges of submarginal lacinia setae, but could not be confirmed with reared and associated specimens. One *I. sobria* male larva from Williams Fork, Grand County, Colorado, four larvae from Rio Fernando de Taos, Taos County, New Mexico, and one exuvia from Tye Spring, Skamania County, Washington, had two close set lacinia submarginal (A) setae. This character would overlap with the lower range observed for *I. tilasqua* (Table 2). Another male larva from Marion Creek, Linn County, Oregon, possessed 5 lacinia submarginal (A) setae, and two submarginal (B) setae. However, all the above male larvae were identified as *I. sobria* because they possessed long, thin, apically pointed setae on the maxillary palp basal segments 2–3 and inverted V shaped light interocellar marks.

***Isoperla sordida* Banks**
(Figs. 2p, 18a-h, 20p)

Isoperla sordida Banks 1906, 38:337. Holotype ♂, Los Angeles Co., CA, USA.

Isoperla sordida: Szczytko & Stewart 1979, 32:100-104. ♂, ♀, larva (from ♀ exuvia), ovum.

Material examined. CALIFORNIA: **Mono Co.**, Coldwater Creek, Coldwater Campground, Inyo National Forest, 9000 feet, 16/VIII/1959, C. Alexander, ♂ everted, ♀ (NMNH); Coldwater Campground, Inyo National Forest, 4.7 mi S Mammoth Lakes (Hwy 203), 26/VII/2010, J. Sandberg, Larvae (reared); 08/VIII/2010, ♂♀, Larvae (reared); 07/IX/2010, ♂♀; 09/VIII/2011, J. Harrington, A. Montalvo, J. Sandberg, Larvae; McKay Creek, ~3.6 mi above Sardine Creek, 31/VI/2008, Larvae (ABL); **Nevada Co.**, Bog Spring – Sagehen Creek, Near Hobart Mills, 6300 feet, 14/IX/1965, A. Sheldon, ♀ (NMNH); **San Bernardino Co.**, ?, Hurkey Creek Campground, San Jacinto Mts, 4300 feet, 01/VII/1958, C. Alexander, ♂♀ (poor condition) (NMNH);



Figs. 18a-h. *Isoperla sordida* nymph and ventral maxilla, Fall River, Deschutes County, OR. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, Dorsal seta DS, Dorsal surface setae DSS, and Thin marginal seta TMS. White bars = 1 mm, 18e-f 100x, 18g 200x, and 18h 400x.

OREGON: **Deschutes Co.**, Fall River, Fall River Campground, Hwy 42 (S Century Dr), 13 mi (20.9 km) E Hwy 97, 28&31/V/2008, J. Sandberg, ♂♀, Larvae (reared); **Linn Co?**, McKenzie River, Bridge near Clear Lake, 07/X/1965, S. Jewett Jr., ♀ (NMNH); WASHINGTON: **?County**, **?**, Silver Fir Camp, Mt Baker, 1800 feet, 13/VIII/1947, C. Alexander, ♂ (NMNH).

Male larva. Body length of mature larva 11–13 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus indistinct, connected to light frontoclypeus area by a broad median longitudinal light band, lateral thin arms with nearly parallel margins connected to median light band, directed posterolaterally and extending to antennal bases; posterior ocelli usually with partially enclosed large light areas along outer lateral margins, occasionally light areas small and completely enclosed; interocellar area variable, from completely dark to partially light, completely enclosed by dark pigment and not extending past posterior ocelli; occiput with irregular spinulae band extending from below eye to near median epicranial suture, not enclosed completely by dark pigment (Fig. 18a). **Lacinia** bidentate, total length 856–992 μm (Figs. 2p, 18e-h, Tables 2-4); submarginal row (A+B) with 3–4 setae, groups A-B interrupted by gap below subapical tooth (SAT) inner margin (Fig. 18g); 1 submarginal seta (A) located at base of apical tooth (AT) inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin sometimes obstructed from view by AT, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT or submarginal setae (B) (Figs. 18g-h); 2–3 submarginal setae (B) located past SAT inner margin (Fig 18h); 8–11 marginal setae (C), initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 18e); 41–67 ventral surface setae (D) forming dense longitudinal band below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length, setae closest to inner margin protrude laterally past lacinia margin (Fig. 18f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal

band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 18f). **Galea** with 20–26 setae in sparse ventral row, apex with 2–5 setae. **Maxillary Palp** segments 2–3 with curved, apically pointed setae. **Pronotum** with light median area bordered by wide dark pigment bands, discs each with large, completely enclosed light areas or “windows”, fine dark clothing setae and lateral margins without broad light bands (Fig. 18b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 18c). **Legs** with numerous fine dark clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated on dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20p); tibia with faint transverse bands near proximal end. **Abdominal terga** variable, usually with two distinct longitudinal dark stripes; wide light median longitudinal band sometimes bisected with faint, light brown median longitudinal band; lateral pair of dark longitudinal stripes usually not extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 18d).

Distribution. Canada: Alberta, British Columbia; USA: Alaska, California, Idaho, Montana, Oregon, and Washington. Only recently confirmed in eastern slope Sierra Nevada streams at elevations greater than 1524 m.

Diagnosis. *Isoperla sordida* male larvae are distinct among other western *Isoperla* species with 1–4 submarginal row (A) setae by having a lacinia with 41–67 ventral surface (D) setae (Figs. 18e-f), pronotal discs with large distinct window like light areas (Fig. 18b), and femora with a sparse row of silky setae (Fig. 20p).

Remarks. The type locality for this species is Los Angeles County, California, and is the only specimen of this species known from this county. In Oregon, emergence is in late spring to early summer. In California, emergence occurs in late summer to fall and distribution appears restricted to the eastern Sierra Nevada range high elevation spring fed or snow melt streams above 1524 m.

Isoperla tilasqua Szczytko & Stewart
(Figs. 2q, 19a-h, 20q)

Isoperla tilasqua Szczytko & Stewart 1979, 32:60-61. ♂, ♀, ovum.

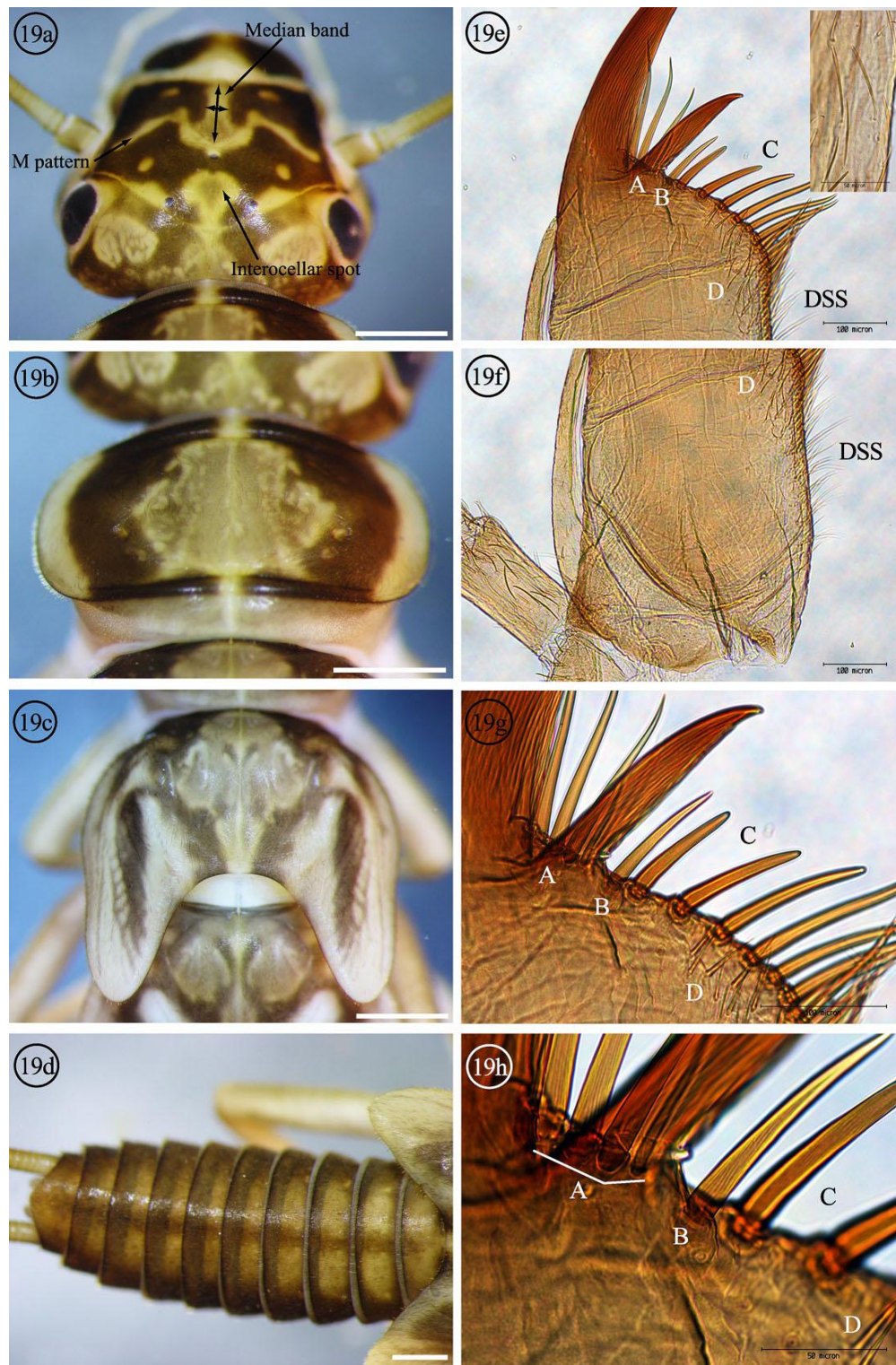
Isoperla tilasqua: Szczytko & Stewart 2004, 130(2):236-237. Larva (reared).

Material examined. TYPES: *I. tilasqua* Holotype ♂, Oregon: **Benton Co.**, Oak Creek, 13-16/VI/1968, ?collector (NMNH #76346); Paratype ♀, Same as Holotype, 7-10/VI/1968; **Additional Specimens.** CALIFORNIA: **Siskiyou Co.**, Sacramento River, Headwater, Mt. Shasta, 29/V/1967, S.G. Jewett Jr., ♀ (NMNH); OREGON: **Benton Co.**, Oak Creek, Trap 2, 6.5 mi NW Corvallis, 1 mi N Fish Lab 650 feet, 19-22/VI/1968, C. Kerst, ♀ (looked more like *I. sobria*) (NMNH); **Clackamas Co.**, Still Creek, Still Creek Campground, Mt Hood, 10/VI/1955, 17/VI/1967, S.G. Jewett Jr., ♀ (NMNH); **Grant Co.**, ?, Trout Meadows, 5500 feet, 09/VII/1967, J. Baker, ♀ (NMNH); **Umatilla Co.**, Meacham Creek, Upstream (west) of Hwy 84 bridge, 30/V/2008, 22/V/2011, J. Sandberg, Larvae (reared).

Male larva. Body length of mature larva 10–11 mm. **Dorsum of head** with contrasting pigment pattern and fine dark clothing setae, anterior frontoclypeus margin unpigmented; light M shaped pattern anterior to median ocellus connected to light frontoclypeus area by a median longitudinal light band, its width approximately half the posteromedian portion of the light M shaped pattern, lateral thin arms with nearly parallel margins connected to median light band, directed posterolaterally and extending to antennal bases; posterior ocelli with completely enclosed medium sized light areas along outer lateral margins, extending laterally above epicranial suture in fresh specimens; in older preserved specimens, posterior light brown band becomes faded; interocellar area partially light, an irregular shaped light area connected to posterior head capsule by thin light band; occiput with irregular spinulae band extending from below eye to near median epicranial suture, usually enclosed completely by dark to light brown pigment (Fig. 19a). **Lacinia** bidentate, total length 978-1012 μm (Figs. 2q, 19e-h, Tables 2-4); submarginal row (A+B) with 4–7 setae, groups A-B

interrupted by gap below subapical tooth (SAT) inner margin (Fig. 19g); 2–5 submarginal setae (A) in a close set row beginning at the base of the apical tooth (AT), ending before reaching SAT inner margin, plus 1 thin marginal seta (TMS) adjacent to AT inner margin, sometimes obstructed from view by AT, submarginal setae, or broken, and 1 dorsal seta (DS) located below SAT inner margin, partially obstructed by SAT (Figs. 19g-h); 1–3 submarginal setae (B) located past SAT inner margin (Fig. 19h); 15–20 marginal setae (C) initially long-stout and widely spaced, last few shorter and closer, blending into and difficult to differentiate from dorsal surface setae (Fig. 19e); 36–62 ventral surface setae (D) scattered below submarginal and marginal setae, ending posteriorly at approximately $\frac{3}{4}$ the inner lacinia margin length (Fig. 19f); dorsal surface setae (DSS) forming dense, laterally protruding, longitudinal band on and along inner-lateral margin, ending before posterior-most ventral surface setae (Fig. 19f). **Galea** with 11–19 setae in sparse ventral row, apex with 2–3 setae. **Maxillary Palp** segments 2–3 with curved, apically rounded setae (Inset, Fig. 19e). **Pronotum** with large median light area bordered by thick dark comma shaped bands typical of the *I. sobria* complex, a range of irregular shaped faded light brown areas usually present between the dark commas and fine dark clothing setae distributed evenly except on a few long light rugosities, lateral margins with broad light bands (Fig. 19b). **Meso and metanotum** with contrasting pigment pattern and fine dark clothing setae (Fig. 19c). **Legs** with numerous fine golden clothing setae and scattered erect spines on outer surface of femora, erect spines longest and concentrated along dorsal surfaces; fine silky setae sparse on dorsal surface of femora, numerous and continuous on tibia (Fig. 20q); tibia with faint transverse band near proximal end. **Abdominal terga** usually with three longitudinal dark stripes; wide light median longitudinal band usually bisected with a median thin faded brown stripe; lateral pair of dark longitudinal stripes about twice as wide as median dark stripe, extending to lateral margins; numerous fine dark clothing setae and erect spines scattered dorsally; posterior margin with scattered long and numerous short spines in a concentrated row (Fig. 19d).

Distribution. Oregon, Washington. Occurrence in



Figs. 19a-h. *Isoperla tilasqua* nymph and ventral maxilla, Meacham Creek, Umatilla County, OR. Submarginal setae groups A and B, Marginal setae C, Ventral surface setae D, and Dorsal surface setae DSS. Fig. 5e Inset: Maxillary palp segment 3 with apically rounded long thin setae, 400x. White bars = 1 mm, 19e-f 100x, 19g 200x, and 19h 400x.

California not confirmed.

Diagnosis. *Isoperla tilasqua* male larvae share the typical comma shaped dark pronotal bands common to the *I. sobria* complex (Fig. 19b) and have similar numbers of submarginal (A) setae when compared to *I. sobria* (Table 2). The long, thin apically rounded setae on basal maxillary palpi segments 2–3 (Fig. 19a Inset) are similar to *I. baumanni* (Fig. 5e Inset). It is distinct from these species by having a partially light interocellar area connected to the posterior margin of head, a continuous light M shaped band above the anterior ocellus, and a relatively thin median longitudinal light band extending from the anterior ocellus to the light frontoclypeus area (Fig. 19a).

Remarks. The Mt. Shasta *I. tilasqua* female in the NMNH from California may be the first record for the state. The female western *Isoperla* taxonomy is known, but variations in the length and shape of the subgenital plate are possible. *Isoperla sobria* females from California and Oregon had elongate subgenital plates with basolateral margins nearly parallel and rounded apical margins. Eight *I. tilasqua* females reared from Meacham Creek, Umatilla County, Oregon, all had subgenital plates with median invaginations similar to *I. gravitans* (Fig. 111 in Szczytko & Stewart, 1979), but the lateral margins, similar to *I. sobria*, were nearly parallel. A reared or recently field collected male will be required to confirm this interesting and possible range extension.

DISCUSSION

The number of *Isoperla* species known from California is reduced from 16 to 15, with the new synonym *I. karuk* placed under *I. roguensis* (Table 1). The larval description for *I. baumanni* in Szczytko & Stewart (2004) was determined to be equivalent to *I. bifurcata* in Bottorff et al. (1990) based upon reared and correlated material from Domingo Springs, California. And *I. baumanni* is tentatively placed in the *I. sobria* complex based upon adult male and larval characters but requires the ovum description.

For convenience of discussion, the larvae of this study can be sorted into three morphological groups based upon the setae of the lacinia submarginal row (not intended to reflect potential phylogenetic groupings):

- 1) Species without a gap between submarginal row groups (A) and (B) (Fig. 4h, *I. adunca*,

- 2) Species with a gap between submarginal row groups (A) and (B) and with 2–7 close set submarginal row (A) setae (Figs. 5h, 19h, *I. sobria* complex) except *I. miwok* with 1 submarginal (A) seta, and
- 3) Species with a gap between submarginal row groups (A) and (B) and with 1–2 widely spaced submarginal row (A) setae (all other species), or submarginal row (A) and (B) regularly spaced (*I. muir*).

For the species included in group three above, several are distinctive using other lacinia characters (*I. muir*, *I. miwok*, and *I. pinta*), lacinia ventral surface setae (D) (*I. denningi*), or fine silky setae of the femora and tibia and pigment patterns (all other species). The identification of the *I. marmorata* complex, *I. sobria* complex, *I. sordida* and *I. quinquepunctata* rely in part, upon the dorsum of head and pronotal pigment patterns which will be of limited usefulness for older preserved specimens.

The pigment patterns of preserved larvae (more than a few years old) have limited usefulness because pigment fades rapidly in ethanol and normal variation. Some larvae darkened in ethanol. Freshly preserved specimens can be placed into six groups based upon pigment patterns:

- 1) Pronotal discs each with wide dark bands (Figs. 8b, 10b, 16b, *I. marmorata* complex).
- 2) Pronotal discs each with comma shaped lateral dark bands (Figs. 5b, 11b, 17b, 19b, *I. sobria* complex).
- 3) Abdomen without longitudinal stripes (Figs. 4d, 9d, *I. adunca* and *I. laucki*).
- 4) Pronotum with variable and small light markings resembling small windows (Figs. 3b, 12b, 15b, *Isoperla quinquepunctata* complex).
- 5) Pronotum with a distinct pattern of light rugosities (Figs. 6b, 13b, *I. bifurcata*, *I. muir*).
- 6) Pronotum with large light markings resembling large windows (Fig. 18b, *I. sordida*).

The *I. marmorata* complex shared similar pigment patterns, ventral lacinia surface setae (D) counts, and femora-tibia fine silky setae characters. This made identification difficult; but by using the presence of the M shaped light pigment pattern, *I. marmorata* (Fig. 10a) could be separated from *I. fulva* (Fig. 8a) and *I. roguensis* (Fig. 16a). The *I. sobria* complex shared comma shaped pronotal pigment bands, but *I.*



Figs. 20a-q. *Isoperla* front right leg habitus, Larvae, 32–40x, Bar = 1mm. 20a. *I. acula*; 20b. *I. adunca*; 20c. *I. baumanni*; 20d. *I. bifurcata*; 20e. *I. denningi*; 20f. *I. fulva*; 20g. *I. laucki*; 20h. *I. marmorata*; 20i. *I. miwok*; 20j. *I. mormona*; 20k. *I. muir*; 20L. *I. pinta*; 20m. *I. quinquepunctata*; 20n. *I. roguensis*; 20o. *I. sobria*; 20p. *I. sordida*; 20q. *I. tilasqua*.

miwok (Figs. 11g-h) differed by having only 1 lacinia submarginal row (A) seta versus 2–7 close setae (*I. baumanni*, *I. sobria* and *I. tilasqua*). A combination of

characters, including distribution was tentatively used to separate these three species. The maxillary palp basal segments 2–3 possessed a few thick, stout

setae and many long, thin setae scattered over most of each segment ventrally. These setae had blunt, apically rounded tips in *I. baumannii* and *I. tilasqua* (Figs. 5e Inset, 19e Inset), and apically pointed tips in *I. sobria* (Fig. 17e Inset). A new non-pigment character will be necessary to reliably separate these species if the dorsal head patterns are determined to overlap. The pigment pattern of *I. adunca* (Fig. 4b) is distinct from *I. laucki* (Fig. 9b) in that the pronotum lacks a pattern and is generally light brown, whereas the *I. laucki* pronotum possesses a series of light rugosities near the median longitudinal light band. Additionally, the M shaped head pattern is incomplete in *I. adunca* (Fig. 4a) and complete in *I. laucki* (Fig. 9a). The pronotal pigment patterns of the three California *I. quinquepunctata* complex species were somewhat similar (Figs. 3b, 12b and 15b) and are separated by the number of lacinia ventral surface setae, femora and tibia fine silky setae, and pigment patterns of the head and abdomen. *Isoperla bifurcata* (Figs. 6a, 6d) is distinct from *I. muir* (Figs. 13a, 13d) in having an incomplete light M shaped head pattern and abdomen with a nearly regular median longitudinal light stripe. *Isoperla sordida* was the only California species with large light window like areas located centrally on each disc (Fig. 18b).

The current study of larval maxillae, leg setation and pigment characters provides support for the adult species complexes of Szczytko & Stewart (1979). The non-pigment characters described in this study proved useful in larval species identification but were not sufficient to separate every species. Therefore, this study remains tentative until other characters can be elucidated.

ACKNOWLEDGEMENTS

Much thanks and gratitude to Stan Szczytko and Ken Stewart for their 1979 comparative study of western *Isoperla* and subsequent species descriptions. My appreciation to Richard Bortorff for his outstanding work in California *Isoperla*. William Hilsenhoff and Steven Billmyer provided the first *Isoperla* larval species key for Wisconsin using lacinia characters which helped guide this study. Special thanks to Richard Baumann, Boris Kondratieff, Jon Lee and Stan Szczytko for recent material loans confirming the *I. karuk* synonymy and encouragement with this manuscript. I greatly

valued and incorporated many of the comments and suggestions provided by two reviewers. Finally I thank those who loaned museum materials or who helped collect, transport and rear live stoneflies for this and associated *Isoperla* drumming studies.

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Received 25 July 2011, Accepted 29 August 2011, Published 15 September 2011

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Jahr/Year: 2011

Band/Volume: [07](#)

Autor(en)/Author(s): Sandberg John B.

Artikel/Article: [The Isoperla of California \(Plecoptera: Perlodidae\); larval descriptions and a key to 17 Western Nearctic species. 202-258](#)