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THE *ISOPERLA* OF CALIFORNIA (PLECOPTERA: PERLODIDAE); UPDATED MALE DESCRIPTIONS AND ADULT KEYS FOR 18 WESTERN NEARCTIC SPECIES

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ABSTRACT
The adults of 18 western Nearctic species of the stonefly genus *Isoperla* Banks from California, Colorado, Oregon, Washington and Utah were studied. Updated species keys and male descriptions are presented. Three species occurring in adjacent states but not recorded in California, *I. rainiera* Jewett, *I. tilasqua* Szczytko & Stewart and *I. umpqua* Szczytko & Stewart, are included in the descriptions and keys.

Keywords: adult species key, *Isoperla*, western Nearctic

INTRODUCTION

The taxonomy of 20 western Nearctic *Isoperla* species was studied by Szczytko & Stewart (1979). They provided descriptions, species keys to all available life stages, and summarized their work by arranging 19 of these species into five complexes based primarily upon characters of the aedeagus and ovum. In their study, two methods for everting the aedeagus were provided (one for live males and another for alcohol preserved males), and we describe the difference between these methods for the first time in this study. Subsequent western Nearctic *Isoperla* studies provided descriptions of new species, descriptions of previously undescribed life stages, regionally revised descriptions, distributions, and a new name for a nomen nudum (Baumann & Lee 2009; Bottorff et al. 1990; Huntsman et al. 1999; Kondratieff & Baumann 2002; Szczytko & Stewart 1984, 2002, 2004, 2013). Stewart & Oswald (2006) provided a key to the adults of 11 species recorded from Alaska and adjacent Canadian provinces.

Currently, 28 *Isoperla* species are recognized from the western Nearctic (Table 1) and 14 of these species have been confirmed in California (Sandberg 2011a, 2011b). This study examines the reared and collected adults from those studies to provide updated adult species keys for California. Adult *Isoperla* taxonomy is based upon characters of the properly everted aedeagus, paraprocts, vesicle, posterior terga spinule

Table 1. Systematic list of 28 western Nearctic *Isoperla* species and species complexes based upon male characters.

Species Complex	Western Nearctic Species	Adult Character					
		P	**S**	**V**	**TS**	**PL**	**PS**
I. quinquepunctata	*I. acula* Jewett 1962	A	PF	R	P	> 1-2	GS
	I. jewetti Szczytko & Stewart 1979		A	L	A	?	?
	I. longiseta Banks 1906		A	L	P	?	?
	I. mormona Banks 1920		PF	T	P	≈ 1-2	AB
	I. quinquepunctata (Banks 1902)		A	L	P	≈ 1-2	GB
I. phalerata	*I. phalerata* Needham 1917		A	L	?	?	?
	I. pinta Frison 1937				P	≈ 1-2	AB-SB
I. sobria	*I. baumanni* Szczytko & Stewart 1984		P	L	A	≈ 1	AB
	I. gravitans (Needham & Claassen 1925)			L		?	?
	I. miwok Bottorff & Szczytko 1990			VE		≈ 1-2	AB
	I. sobria (Hagen 1874)			VE		≈ 1-2	AB
	I. tilasqua Szczytko & Stewart 1979			L		≈ 1	AB
I. marmorata	*I. fulva* Claassen 1937	P	P	L		≈ 1-2	AB
	I. marmorata Needham & Claassen 1925						GB
	I. roguensis Szczytko & Stewart 1984						ATS
I. sordida	*I. adunca* Jewett 1962		A	PE		≈ 1-2	GB
	I. bifurcata Szczytko & Stewart 1979						AB
	I. denningi Jewett 1955						GB
	I. fusca Needham & Claassen 1925					?	?
	I. petersoni Needham & Christenson 1927					≈ 1-2	GB-H
	I. rainera Jewett 1954						GS
	I. sordida Banks 1906						GB
	I. umpqua Szczytko & Stewart 2013				P		GB
Unassigned	*I. decolorata* (Walker 1852)	A	A	PE	A	?	?
	I. katmaiensis Szczytko & Stewart 1979	A	A		A	?	?
	I. marlynia (Needham & Claassen 1925)	A	A		A	> 1-2	GS
	I. laucki Baumann & Lee 2009	P	P		A	≈ 1-2	GB
	I. transmarina (Newman 1838)	A	A		A	≈ 1	AB

P=Aedeagus sclerotized process, **S**=Aedeagus spinule patch, **V**=Vesicle, **TS**=Tergal spinulae or stout setae, **PL**=Paraproct length, **PS**=Paraproct shape, A=Absent, P=Present, PF=Fine spinulae present, PM=Minute spinulae present, R=Rectangular, T=Trapezoidal, L=Lobe, PE=Pedunculate, VE=Vestigial, > 1-2=PL > cercal segments 1-2, ≈ 1-2=PL subequal to cercal segments 1-2, ≈ 1=PL subequal to first cercal segment, GS=Tapering gradually to sharp points, AB=Tapering abruptly to blunt points, GB=Tapering gradually to blunt points, ATS=Tapering abruptly to tiny sharp points, SB=Secondarily barbed, H=Hook shaped, ?=Character not described.

patches, and the female subgenital plate shape. The following keys use wing and abdomen pigmentation, distributions, two aedeagal eversion methods, and other morphologic characters to separate closely related species. Our objective for this comparative study is to update the previous western Nearctic species revision (Szczytko & Stewart 1979) and California species key (Jewett 1960) by providing color photomicrograph plates and revised descriptions based upon recently collected or reared material using a standardized aedeagal eversion method.

MATERIALS AND METHODS

The majority of adults examined for this study were reared from mature larvae collected from sites

listed in previous studies (Sandberg 2011a, 2011b). Aedeagus eversions were all conducted with live males in the lab following methods provided by Sandberg (2011b) and Sandberg & Stewart (2005). Additional collection records are presented to augment the known distribution of *Isoperla* in California.

The live everted and fixed aedeagi of six species (*I. baumanni* Szczytko & Stewart 1984, *I. fulva* Claassen 1937, *I. marmorata* Needham & Claassen 1925, *I. miwok* Bottorff & Szczytko 1990, *I. roguensis* Szczytko & Stewart 1984, and *I. tilasqua* Szczytko & Stewart 1979) were cleared in 10% KOH. Soft tissues dissolved in approximately 1-2 hours, allowing for examination of inverted, internal membranous tube-like processes within the aedeagal body. Further eversion of the inverted tube-like processes was attempted by holding the proximal abdomen with one forceps, and applying pressure and pulling towards the cerci with a second forceps. Further eversion usually resulted in bursting the outer aedeagal membrane or abdomen and was only partially successful for *I. baumanni*.

Color photomicrographs were taken using a Zeiss Stemi SV6 fitted with an intermediate phototube, 1.0x camera adapter (for increased photographic magnification), and either a Lumenera Infinity 1-2C (1/2 inch CMOS sensor) or an Infinity 2-2C (1/1.8 inch CCD sensor) video camera and Infinity Analyze image capture software.

The figures of adult male characters were produced from a series of 5-35 photomicrographs taken at successively deeper focal planes that were combined and simultaneously focused using Helicon Focus version 5.3 software (image processor designed to cope with the shallow depth of field problem). Photographic adjustments were made using the Curves and Levels control in Adobe Photoshop CS3. Photomicrographs of cleared aedeagi were obtained using a 0.5x camera adapter (normal magnification and increased light sensitivity).

The updated California and other materials examined are deposited in the Aquatic Bioassessment Lab Collection, California State University, Chico, California (ABLC); C.P. Gillette Museum of Arthropod Diversity, Fort Collins, Colorado (CSUC); and the John B. Sandberg Collection, Paradise, California (JBSC).

RESULTS

Twenty-two western Nearctic species placed into species complexes by Szczytko & Stewart (1979, 1984), Bottorff et al. (1990), and Sandberg (2011b), and six unassigned species are described with the six primary characters used in this study (Table 1). These as well as additional male and female characters used in this study are defined below. The male species descriptions are not complete descriptions, and intended to supplement those in previous studies (Baumann & Lee 2009; Bottorff et al. 1990; Szczytko & Stewart 1979, 1984, 2002, 2004, 2013).

Taxonomic Characters

Male

- *Aedeagus sclerotized process*. When present, projects from the posteromedian margin of aedeagus, visible after eversion. The process shape or size usually provides conclusive species identification. *Isoperla fulva* and *I. roguensis* have noticeable intraspecific variation in the shape and width of the process apex.

- *Aedeagus shape and distinct lobes*. The membranous aedeagal body ranges from possessing no discernible lobes to 4-5 distinct lobes along posterior, dorsal and anterior margins. In this study, the thin extended apical lobe or lobes described for *Isoperla baumanni*, *I. fulva*, *I. miwok*, *I. roguensis*, and *I. tilasqua* remained inverted as internal processes (Bottorff et al. 1990; Szczytko & Stewart 1979, 1984, 2002, 2004). This was the result of using two different eversion methods: the eversion of the aedeagus of live males (the current study method) vs. the eversion of the aedeagus of alcohol preserved males by clearing in heated 10% KOH and mechanically everting the aedeagus (Szczytko & Stewart 1979).

- *Distinct aedeagal spinulae patches*. Variously shaped and positioned patches of distinct spinulae on aedeagal membrane. Patches usually easily detected under the dissecting microscope when present, but not to be confused with evenly spaced minute spinulae covering larger areas of the aedeagal membrane (not described in this study due to their minute size).

- *Spinulae or stout setae patches on abdominal terga 8-*

10. Long fine light, short stout, or stout dark spinulae present on terga 8-9, or only tergum 9 (*I. acula* Jewett 1962, *I. mormona* Banks 1920, *I. pinta* Frison 1937 and *I. umpqua* Szczytko & Stewart 2013). Concentrated patches of stout pale setae present near posterolateral margins of terga 9-10 (*I. quinquepunctata* (Banks 1902)). The patches of stout setae are variable in *I. quinquepunctata* and spinules small in *I. umpqua*.

- *Brush setae along posterolateral abdominal margins*. Grouped microtrichia along laterodistal margins of segments eight or nine (Zwick 2000). Flattened brush setae occur on at least segments 6-9 and once on segment 10. The size of brush setae decreases progressively on segments anterior of eight, making the determination of abdominal segment range difficult.

- *Paraproct length and shape*. High intraspecific variation made exact description difficult. The general shape always curved dorsally and the curved paraproct length, if straightened, is compared with either the first or the combined length of the first and second cercal segments. In an attempt to provide increased shape details, two paraproct lateral margin (from approximately mid-length to apex), and two paraproct apex shape character states were described and are consistent in both dorsal and lateral views. These include abruptly tapering lateral margins (appearing triangular), gradually tapering lateral margins (appearing nearly parallel), apex with blunt tip, and apex with sharp tip.

- *Vesicle shape*. Sclerotized posteromedian expansion of sternum eight. Variable in size and shape; the character states for shape include lobe-like, pedunculate, rectangular and trapezoidal. Lobe-like vesicles were broadest at base with rounded lateral margins and broadly rounded apices (*I. quinquepunctata* was the only exception). Pedunculate vesicles were constricted near the base, with expanding and concave lateral margins, and rounded apices.

Female

Adult females were separated primarily by the shape and size of the subgenital plate. Pigment characters were used secondarily and are not reliable for use in older alcohol preserved material. The following species, *I. bifurcata* Szczytko & Stewart 1979, *I. fulva*, and *I. roguensis* could not be reliably identified using these characters.

Keys to the *Isoperla* of California (including *I. rainiera*, *I. tilasqua* and *I. umpqua*)

Males

1 Pronotum checkered black on yellow; aedeagus without sclerotized process; paraprocts abruptly tapering to blunt apical tips, usually secondarily barbed ventrally; vesicle a broadly rounded lobe, wider at base then apex (Figs. 11a-d) ..…... ***I. pinta***

1′ Pronotum without checkered pigment pattern, aedeagus, paraprocts and vesicle variable …..... **2**

2 Aedeagus without posterior sclerotized process (Figs. 1, 3, 9-12, 15, 17) ……..……...…… **3**

2′ Aedeagus with variable posterior sclerotized process (Figs. 2, 4-8, 13-14, 16, 18) ……...……. **9**

3(2) Vesicle absent or weakly produced (Figs. 9d, 15d) ……...…….…… **4**

3′ Vesicle present and variably shaped (Figs. 1d, 3d, 10d, 13d, 18d) ……..……..…….. **5**

4(3) Aedeagal posterior margin with a median patch of spinulae (Figs. 15a-c); apex usually with two small, pointed lobes (Figs. 15a-c) …….. ***I. sobria***

4′ Aedeagal posterobasal margin with a median patch of spinulae concentrated into two distinct longitudinal bands (Figs. 9a-b); and a second posteroapical patch of spinulae above posterior lobe (Figs. 9a, c) ……..….. ***I. miwok***

5(3) Ninth tergum with short stout spinulae (sometimes arranged in a bipartite patch) or ninth and tenth terga with distinct patches of long stout setae near posterior margins (Figs. 1c, 10c, 12c) …….……...….. **6**

5′ Ninth and tenth terga without spinulae, long setae usually scattered ……...……..….. **8**

6(5) Vesicle rounded apically, base broader than apex, occasionally appearing constricted at middle; paraproct length if straightened, subequal to combined length of first two cercal segments, tapering gradually to blunt apices; posterolateral margins of ninth and tenth terga with patches of long stout setae, fewer and smaller on tergum ten (Figs. 12a-d) ……...….. ***I. quinquepunctata***

6′ Vesicle truncated or rectangular apically; paraproct length and shape variable; ninth and tenth terga with scattered fine setae, ninth tergum with mesal patches of short stout spinulae (Figs.

1, 10) ……..…..... **7**

7(6) Vesicle rectangular, length half as long as wide (Fig. 1d); apical 1/3 of aedeagus tube-like, directed ventrally, covered with minute spinulae and a posterior pair of finer spinule patches divided or joined apically, apex a complex nipple-like tip (Figs. 1a-c); paraproct length if straightened greater than combined length of first and second cercal segments, tapering gradually to sharp apices (Fig. 1c) ……..… ***I. acula***

7′ Vesicle trapezoid shaped, about as long as wide (Fig. 10d); apical 1/2 of aedeagus tube-like, directed posteriorly, covered with minute spinulae and concentrated somewhat above bi-lobed tip (Figs. 10a-c); paraproct length if straightened subequal to combined length of first two cercal segments, tapering gradually to blunt apices (Fig. 10c) ..... ***I. mormona***

8(5) Abdomen yellow; when everted live and fixed in hot water, aedeagus with one large patch of spinulae concentrated below posterobasal lobe (Fig. 3b), a long thin patch along posteroapical margin (Fig. 3c), apex bulbous, deeply inverted, and without a pair of short apicolateral lobes; when cleared in KOH, apex with a single inverted tube-like process (Fig. 20a), CA-Domingo Spring ……..……..…..... ***I. baumanni***

8′ Abdomen dark; when everted live and fixed in hot water, aedeagus with one large patch of spinulae concentrated below posterobasal lobe (Fig. 17b), a long thin patch along posteroapical margin (Fig. 17c), apex bulbous, deeply inverted, and usually with one pair of short sharp apicolateral lobes near apex (similar to *I. sobria*); when cleared in KOH, apex with two inverted tube-like processes (Fig. 20f), OR, WA ……... ***I. tilasqua***

9(2) Vesicle a broadly rounded lobe, wider at base then apex (Figs. 6d, 8d, 14d, 16d) ……...…. **10**

9′ Vesicle pedunculate, width subequal to length, constricted near base with curved lateral margins, and apex variable (Figs. 2d, 4d, 5d, 7d, 13d, 18d) ……..……..…..… **13**

10(9) Aedeagus with at least one patch of stout spinules above sclerotized process (Figs. 6a, 8b, 15a); apex of sclerotized process rounded in lateral view (Figs. 6a, 8a, 15a), distal margin either thin or expanded in posterior view (Figs. 6b, 8b, 15b) ……..……...…..… **11**

10′ Aedeagus without a spinule patch above sclerotized process (Fig. 16a); apex of sclerotized process expanded, flattened and projecting dorsally in lateral view (Fig. 16b), bifurcate subapically with two ventrally directed rounded lobes in posterior view (Fig. 16b inset), width of lobes 0.18-0.20 mm ……..... ***I. sordida***

11(10) A single patch above sclerotized process composed of fine pale spinules; apex of sclerotized process rounded in lateral view (Figs. 8a-b), distal margin thin and blade-like in posterior view (Fig. 8b) ….……***I. marmorata***

11′ Spinule patch either single or triple and usually dark (Figs. 6c, 14c); apex of expanded sclerotized process rounded in lateral view (Figs. 6a, 14a), distal margin expanded slightly in posterior view (Figs. 6c, 14c) ……..... **12**

12(11) A single spinule patch above sclerotized process (Figs. 6a & c) ..…… ***I. fulva***

12′ One bi-hemispherical shaped spinule patch above sclerotized process and a pair of smaller rounded patches laterally (Figs. 14a-c) …… ***I. roguensis***

13(9) Aedeagal sclerotized process bifurcate in posterior view (Figs. 4-5) ……..……. **14**

13′ Aedeagal sclerotized process not bifurcate in posterior view (Figs. 2, 7, 13, 18) …….. **15**

14(13) Sclerotized process with long apically pointed bifurcate arms; length of projecting process greater than 0.5 mm (Fig. 4a); abdomen mostly brown ……..……... ***I. bifurcata***

14′ Sclerotized process with short rounded bifurcate lobes; length of projecting process less than 0.5 mm (Figs. 5a-b); width of bifurcate apicolateral lobes 0.09-0.10 mm; abdomen mostly yellow ……..... ***I. denningi***

15(13) Posterior margin of aedeagus with elliptical shaped patch of long stout spinulae separated from and above sclerotized process; sclerotized process digitate, with nearly parallel dorsal and ventral margins in lateral view, apex narrowly rounded (Figs. 7a-c) ..…….….. ***I. laucki***

15′ Posterior margin of aedeagus without a patch of long stout spinulae; sclerotized process otherwise (Figs. 2, 13, 18) ……..……...……..... **16**

16(15) Sclerotized process crescent shaped in dorsal and ventral views (Figs. 13b-c); paraprocts gradually tapering to sharp apices (Fig. 13c) OR,

WA ……..……..…. ***I. rainiera***

16′ Sclerotized process clavate; paraprocts tapering gradually to blunt apices; OR, CA ...…..…… **17**

17(16) Wings hyaline; aedeagus with one distinct lobe (Fig. 18a); sclerotized process length approximately 0.50 mm (Figs. 18a-c); mesoposterior area of 8th and 9th terga with bipartite patches of stout spinulae and long fine scattered setae (Fig. 18c), OR ...……... ***I. umpqua***

17′ Wings tinted; aedeagus with four distinct lobes in lateral view (Fig. 2b); sclerotized process length approximately 0.25 mm (Fig. 2b), spinule patches absent on terga 8-9, CA …….. ***I. adunca***

Females

1 Subgenital plate usually with invagination along apical margin (Figs. 19b-c, 19l-m, 19q-s) .....…. **2**

1′ Subgenital plate usually not invaginated (Figs. 19a, 19d-k, 19n-p) ..…….…. **9**

2(1) Subgenital plate with deep median invagination, the apex 3–4 times wider than depth (Figs. 19b, 19r) ……..... **3**

2′ Subgenital plate with shallow median invagination, the apex 8–10 times wider than depth (Figs. 19c, 19l-m, 19q, 19s) ..……... **4**

3(2) Subgenital plate length less than half the width at base (Fig. 19b) ……...……..… ***I. adunca***

3′ Subgenital plate length approximately half the width at base (Fig. 19r) ……..……..… ***I. tilasqua***

4(2) Subgenital plate apex truncated, with nearly parallel lateral margins (Fig. 19c); deflected ventrally in lateral view, CA-Domingo Spring ……..…. ***I. baumanni***

4′ Subgenital plate apex rounded and not deflected ventrally in lateral view (Figs. 19l-m, 19q, 19s) ……..... **5**

5(4) Subgenital plate width at base approximately half the width of segment 8 and nearly twice that of the subgenital plate length (Fig. 19m) ……..... ***I. quinquepunctata***

5′ Subgenital plate width at base greater than half the width of segment 8 (Figs. 19l, 19q, 19s) …… **6**

6(5) Subgenital plate lateral margins broadly rounded (Fig. 19q) ……..…..…… ***I. sordida***

6′ Subgenital plate with short, nearly parallel lateral margins (Figs. 19l, 19s) ……..…..…… **7**

7(6) Pronotum with checkerboard pattern (Fig. 12d inset) ……...……. ***I. pinta***

7′ Pronotum without checkerboard pattern ……... **8**

8(7) Apical margin of subgenital plate sometimes invaginated (broadly rounded in Fig. 19j), apex reaches approximately mid-length of ninth sternum (CA) …… ***I. miwok*** (in part)

8′ Apical margin of subgenital plate typically invaginated (Fig. 19s), apex not reaching mid-length of ninth sternum (OR) ……... ***I. umpqua***

9(1) Subgenital plate with lateral margins nearly parallel (Figs. 19j, 19p) **10**

9′ Subgenital plate with lateral margins not nearly parallel (Figs. 19a, 19d-i, 19k, 19n-o) **11**

10(9) Subgenital plate width nearly as wide as segment 8 (Fig. 19j) ……...……. ***I. miwok***

10′ Subgenital plate width distinctly less than width of segment 8 (Fig. 19p) ……..……...…… ***I. sobria***

11(9) Subgenital plate triangular (Figs. 19g, 19o) …..…….. ***I. fulva, I. roguensis*** (in part)

11′ Subgenital plate rounded (Figs. 19a, 19d-g, 19h-i, 19k, 19n) ……..……...……..…. **12**

12(11) Subgenital plate width at base approximately 4-5 times that of the length (Figs. 19d-f, 19i, 19n) …….……... **13**

12′ Subgenital plate width at base approximately 2-3 times that of the length (Figs. 19a, 19h, 19k) ……..... **16**

13(12) Subgenital plate completely suffused with dark pigment (Fig. 19n) ……. ***I. rainiera***

13′ Subgenital plate partially patterned with pigment or completely light (Figs. 19d-f, 19i) ……..…. **14**

14(13) Subgenital plate partially patterned with pigment (Figs. 19d, 19f-g) ….. ***I. bifurcata, I. fulva***

14′ Subgenital plate completely light (Figs. 19e, 19i) ……..... **15**

15(14) Subgenital plate width at base approximately 3-4 times the length (Fig. 19e) …… ***I. denningi***

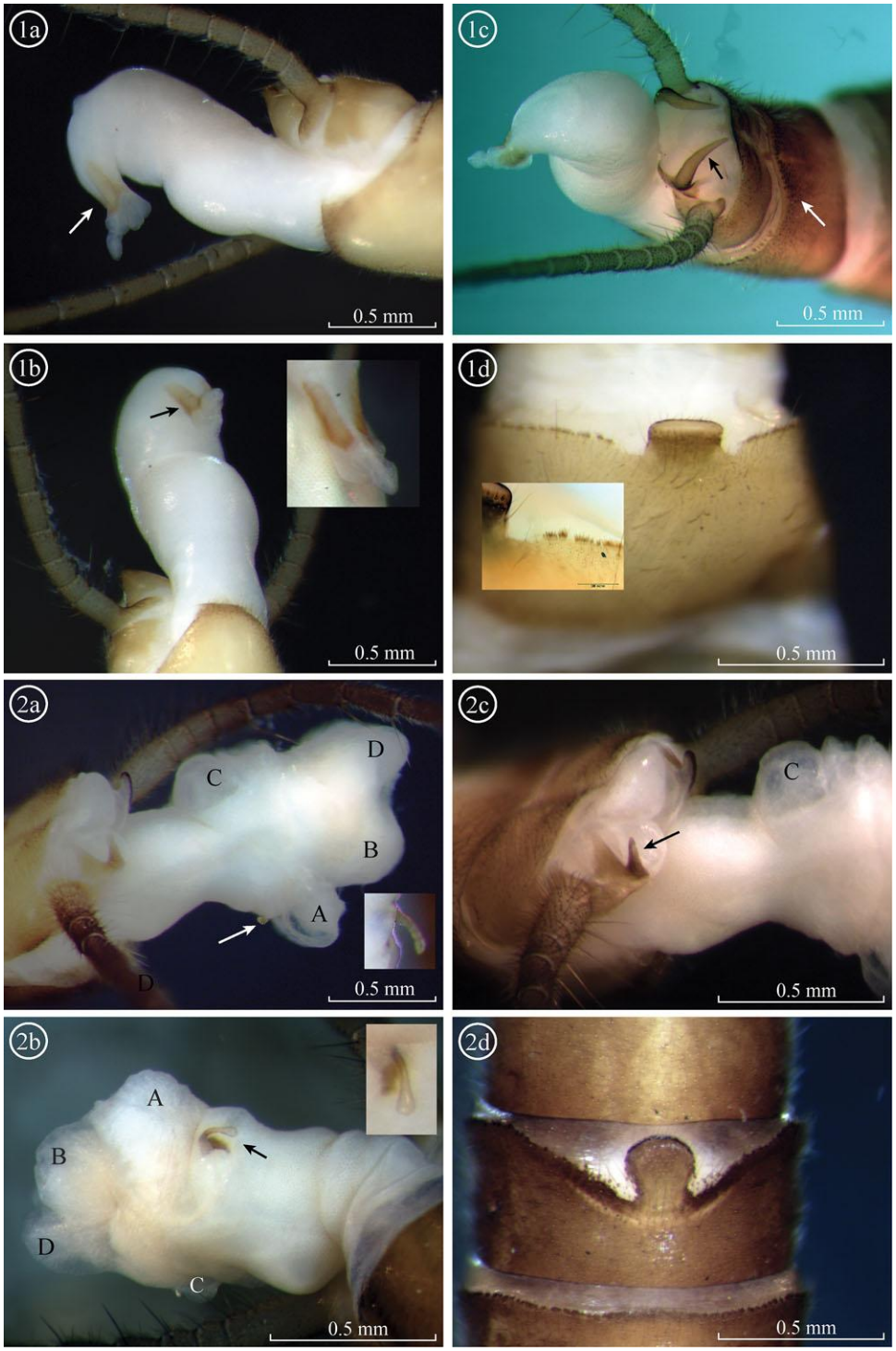
15′ Subgenital plate width at base 6-7 times the length (Fig. 19i) …….…… ***I. marmorata***

16(12) Subgenital plate width at base approximately 3 times as wide than length; apex slightly truncated or broadly rounded (Fig. 19k) ...…… ***I. mormona***

16′ Subgenital plate width at base approximately twice that of the length (Figs. 19a, 19h) …..…. **17**

17(16) Subgenital plate darkly pigmented (Fig. 19h) ……...……. ***I. laucki***

17′ Subgenital plate not darkly pigmented (Fig. 19a) ……... ***I. acula***



Figs. 1-2. Adult male characters of *Isoperla acula,* Deadman Cr., El Dorado Co., CA and *I. adunca,* Campbell Cr. & Trib., Butte Co., CA, 32-50x. Fig. 1a. *I. acula* aedeagus, lateral; fine spinule patch (arrow). Fig. 1b. Aedeagus, ventral; fine spinule patches (arrow & inset-posterior view). Fig. 1c. Paraprocts, (black arrow); abdominal spinules (white arrow). Fig. 1d. Vesicle; brush setae (inset). Fig. 2a. *I. adunca* aedeagus, lateral; sclerotized process (arrow & inset-lateral view). Lobes A: posterobasal, B: posteromedian, C: anterior, D: dorsomedian pair. Fig. 2b. Aedeagus, ventral; sclerotized process (arrow & inset-posterior view). Fig. 2c. Paraprocts (arrow). Fig. 2d. Vesicle.

Isoperla acula Jewett

(Figs. 1a-d)

Isoperla acula Jewett 1962. Holotype ♂, California, Fresno County, Dry Creek, 7 mi NE Academy.

Male. Aedeagus: sclerotized posterior process absent; body a long recurved tube without major lobes, tapering to a multi-lobed apex (Fig. 1a); a pair of long, nearly parallel patches of fine spinulae along posteroapical margin (Figs. 1a-b). Ninth tergum with mesoposterior bipartite to oval patches of stout dark spinulae and long fine scattered setae, tenth tergum with only a few small spinulae (Fig. 1c). Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae (Fig. 1d inset). Paraprocts: curved dorsally, length if straightened longer than combined first and second cercal segments, tapering gradually to long sharp apices (Fig. 1c). Vesicle: rectangular, length half as long as wide (Fig. 1d).

The male of *I. acula* (*I. quinquepunctata* complex) is most similar to *I. mormona* and *I. quinquepunctata*, all lacking an aedeagal sclerotized process (Table 1). However, the similarity in other male taxonomic characters of the three species varies with *I. acula* and *I. mormona* possessing patches of fine spinulae near the apex of aedeagus; vesicle shape varies from lobe-like (*I. quinquepunctata*) to rectangular (*I. acula*) and trapezoidal (*I. mormona*); abdominal terga 9-10 variable posteriorly with patches of stout setae (*I. quinquepunctata*) or patches of stout spinulae and scattered long setae (*I. acula*, *I. mormona*); paraproct length > than first and second cercal segments (*I. acula*) or subequal to first and second cercal segments (*I. mormona*, *I. quinquepunctata*); and paraproct shape variable, tapering gradually to sharp apices (*I. acula*), tapering abruptly to blunt apices (*I. mormona*) and in *I. quinquepunctata*, tapering gradually to blunt apices. The current study *I. acula* description agrees with those of Jewett (1962), Szczytko & Stewart (1979), and Bottorff et al. (1990).

Additional Material Examined. CALIFORNIA, Shasta Co., Rock Creek, West Redding, 05/VI/2011, larvae, (ABLC).

Isoperla adunca Jewett

(Figs. 2a-d)

Isoperla adunca Jewett 1962. Holotype ♂, California, Santa Clara County, 5 mi E Mt. Hamilton.

Male. Aedeagus: sclerotized posterior process present; body with one posterobasal and one posteromedian lobe, dorsomedian apex with a pair of rounded lobes, and one anterior lobe (Fig. 2a); sclerotized process length approximately 0.25 mm, recurved and rod-like, located below posterior lobes (Fig. 2a), and apex clavate in posterior and lateral views (Figs. 2a-b). Abdominal terga 8-9, 9, or 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to first and second cercal segments, tapering gradually to blunt apices (Fig. 2c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 2d).

Isoperla adunca (*I. sordida* complex) shares similar characters with *I. umpqua* (known only from Oregon, and a species that should also be included in the *I. sordida* complex). Both species have a clavate sclerotized process in lateral and posterior views, lack aedeagal spinule patches, possess pedunculate vesicles, and have similar paraproct lengths and shapes (Table 1). Primary differences involve tergal spinulae and two aedeagal characters: *I. adunca* has 4 lobes and *I. umpqua* has one; the sclerotized process length is approximately 0.25 mm for *I. acula* and approximately 0.5 mm for *I. umpqua*; and short stout spinulae present on terga 8-9 for *I. umpqua* only. Lastly, *I. adunca* wings are tinted and the wings of *I. umpqua* are hyaline. The *I. adunca* aedeagus and paraproct shapes differed from those described by Szczytko & Stewart (1979). In the current study, the aedeagus has four distinct lobes in lateral view (Fig. 2a) and paraprocts curved dorsally (Fig. 2c) vs. aedeagus with only one apical lobe and paraprocts deflected downward (Szczytko & Stewart 1979, figs. 159-160).

Isoperla adunca, as with *I. acula* and *I. miwok*, is usually associated with small intermittent streams of the Sierra Nevada foothills from north to south-central California (Bottorff et al. 1990, Sandberg 2011b). The northern most distribution was recently found in Shasta County and the southwestern most

Figs. 3-4. Adult male characters of *Isoperla baumanni*, Domingo Springs, Plumas Co., CA and *I. bifurcata*, Mosquito Spring, Plumas Co., CA, 25-50x. Fig. 3a. *I. baumanni* aedeagus, lateral; large posterobasal spinule patch & thin apical patch (arrows). Lobes A: posterobasal, B: posteromedian. Fig. 3b. Aedeagus, posterior; large basal spinule patch (arrow). Fig. 3c. Paraproct (white arrow); apical thin spinule patch (black arrow). Fig. 3d. Vesicle. Fig. 4a. *I. bifurcata* aedeagus, lateral. Lobes A: posterobasal, B: posteromedian, C: dorsal, D: anterior lobe. Sclerotized process characters 1: base, 2: median arm, 3: bifurcate arms, 4: subapical barb & apical tine. Fig. 4b. Aedeagus, ventral. Fig. 4c. Paraproct (arrow). Fig. 4d. Vesicle.

distribution of *I. adunca* overlaps with *I. denningi* and *I. mormona* in Ventura and San Diego counties. Records for this species from Alameda and Santa Clara Counties are located in the Coastal Range.

California typically experiences high variation in precipitation (Haston & Michaelsen 1979) and 2013 is evidencing to be a drought year (http://www.wrc.dri.edu/). Before completing its life cycle, especially in drought years, *I. adunca* must cope with drying conditions including rapidly warming water temperatures occurring in non-perennial streams. For example, mature larvae of *I. adunca* were collected on 24 April 2013 from Orestimba Creek (Stanislaus County, 119 m asl) when stream temperatures had already reached 26.94°C (L.E. Serpa, per. com.).

Additional Material Examined. CALIFORNIA, Riverside Co., San Juan Creek, 0.4 mi (0.6 km) N Lion Canyon Creek, 19/V/2011, larvae, (ABLC); Santa Clara Co., Tributary to Arroyo Aguague, UCB Blue Oaks Ranch, N37.37189, W121.73289, 06/V/2012, larva (ABLC); Shasta Co., Rock Creek, West Redding, 05/VI/2011, larvae, (ABLC); Rock Creek, at Iron Mountain Rd., 04/V/2009, larvae (ABLC); Stanislaus Co., Orestimba Creek, 19.3 km E Newman, 37.289°N, 121.22008°W, 24/IV/2013, L.E. Serpa, Larvae, (JBSC).

Isoperla baumanni Szczytko & Stewart
(Figs. 3a-d, 20a)

Isoperla baumanni Szczytko & Stewart 1984. Holotype ♂, California, Plumas County, Domingo Spring, Domingo Spring Campground, 6 mi NW Chester.

Male. Aedeagus: sclerotized posterior process absent; body with one posterobasal lobe, one posteromedian lobe and expanded apex, apex deeply inverted (Fig. 3a); one large patch of spinulae concentrated below posteromedian lobe (Fig. 3b), and a long thin patch along posteroapical margin (Fig. 3c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to first cercal segment, tapering abruptly to blunt apices (Fig. 3c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 3d).

The males of *I. baumanni* and *I. tilasqua* are very similar, with the exception of recently preserved specimens. Males of *I. baumanni* have yellow abdominal pigmentation which can be easily separated from the much darker *I. tilasqua*. The aedeagal spinulae and lobe characters are very similar; both species possess one large patch of spinulae concentrated below the posteromedian lobe, a long thin patch along posteroapical margin, and bulbous apex deeply inverted (Figs. 3a-c, 17a-c). *Isoperla tilasqua* differs slightly from *I. baumanni* (live everted) by usually possessing a pair of small apicolateral lobes (similar to *I. sobria* (Hagen 1874)). Males of both species may be identified using the thin extended apical lobe characters illustrated in Szczytko & Stewart (1979, fig. 116; 1984, fig. 53); *I. baumanni* has only one extended tube-like lobe and *I. tilasqua* has two. Sandberg (2011b) suggested that extended lobes are normally inverted internal structures, and evert only when using the KOH clearing-eversion method for preserved males (Szczytko & Stewart 1979). These lobes could not be everted using the live eversion, hot water fixing, and KOH clearing methods described in this study.

The aedeagi of live everted *I. baumanni* and *I. tilasqua* were cleared in KOH to detect the inverted tube-like processes. The internal membrane of a single inverted apical process was visible inside the aedeagus of *I. baumanni* after clearing (Fig. 20a). The apical inverted process could only be partially everted for *I. baumanni*, with the longitudinally striated apex remaining inverted. For *I. tilasqua*, a pair of inverted tube-like processes could be observed within the aedeagus, but could not be everted after clearing (Fig. 20f).

The *I. baumanni* aedeagal shape, stout spinule patches, paraproct and vesicle shape are also similar to *I. gravitans* (Needham & Claassen 1925) in Szczytko & Stewart (1979, figs. 106-110). Sandberg (2011b) also had difficulty separating *I. baumanni* from *I. tilasqua* nymphs using lacinia characters and tentatively placed *I. baumanni* into the *I. sobria* species complex. The three species appear to have locally restricted distributions and further study will be necessary to understand species limits of *I. baumanni*, *I. tilasqua*, and *I. gravitans*.

Isoperla bifurcata Szczytko & Stewart
(Figs. 4a-d)

Isoperla bifurcata Szczytko & Stewart 1979. Holotype ♂, Oregon, Union County, Lick Creek, 6 mi E Medical Springs.

Male. Aedeagus: sclerotized posterior process present; body with one posterobasal lobe, one posteromedian lobe, one large dorsal lobe and one anterior lobe (Fig. 4a); sclerotized process length > 0.5 mm, distal-projecting portion recurved and deeply bifurcate, apices of bifurcate arms with acute points and secondarily barbed (Figs. 4a-c), and length of proximal-attached base (Fig. 4a, 1) less than the total length of distal-projecting median arm (Fig. 4a, 2), bifurcate arms (Fig. 4a, 3), and apical tine (Fig. 4a, 4). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to variable blunt to sharp apices (Fig. 4c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 4d).

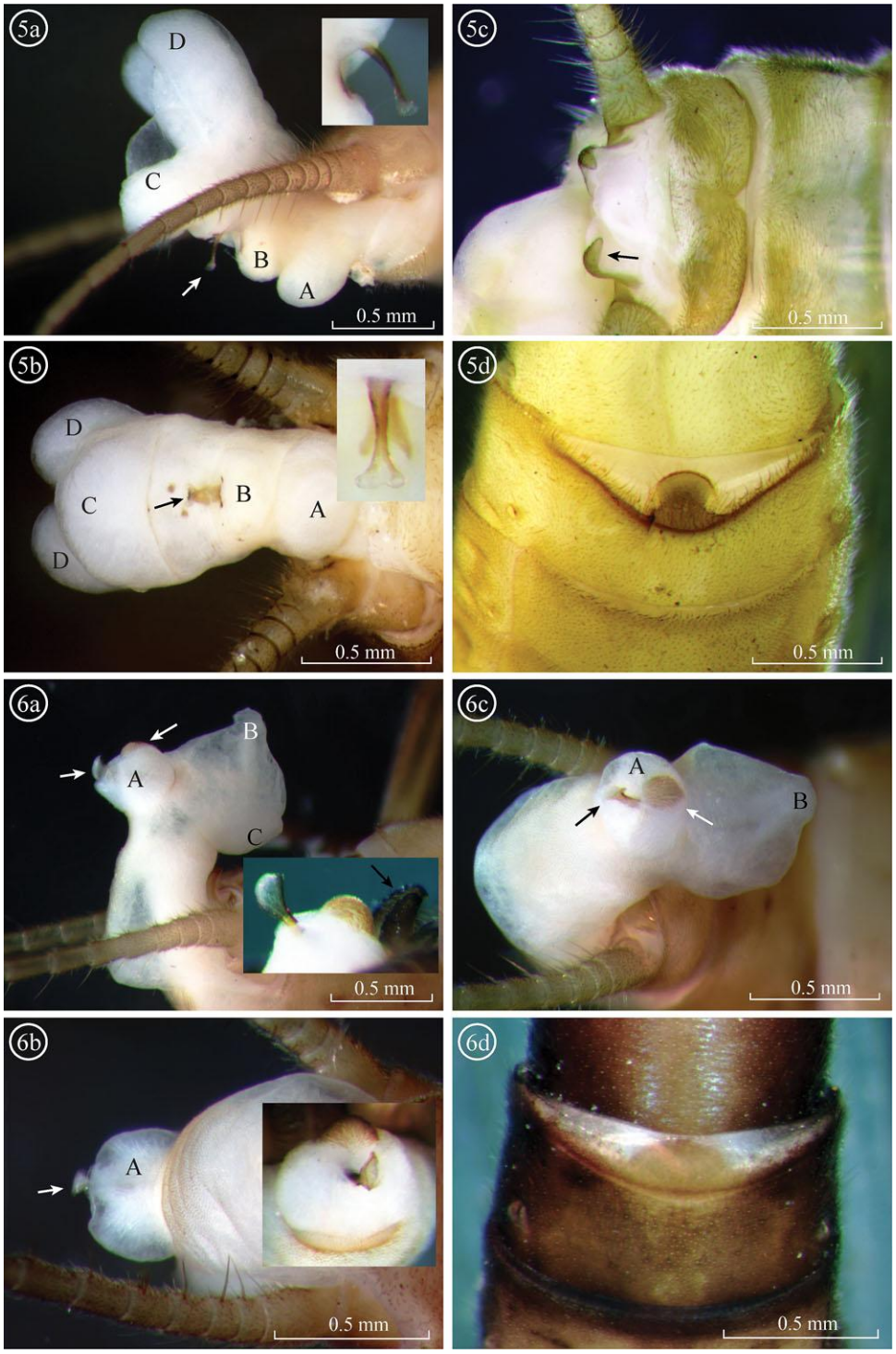
Isoperla bifurcata is most similar to *I. fusca* Needham & Claassen 1925, a species not known to occur in California and not included in this study. The vesicle shape for *I. bifurcata* differed from the previous description. In this study, the pedunculate vesicle length is subequal to width, and rounded at apex (Fig. 4d). In Szczytko & Stewart (1979, fig. 164), the vesicle width appears greater than length and the apex is both described and illustrated as truncate.

The *I. bifurcata* sclerotized process description and couplet 20 of the key to the males in Szczytko & Stewart (1979) are imprecise. The ambiguity is caused by not clearly defining the "base" character (there are two possible interpretations), and two different proximal-attached "base" lengths are illustrated in lateral view and upside down posterior view in Szczytko & Stewart (1979, figs. 165C & 168, respectively). The written description provides one length character: "arms of apical fork extending same length as base…(figs. 165C & 168)". Figure 165C (in Szczytko & Stewart 1979) is a lateral view of the process and does not provide a clear view of the apical fork length, but does indicate the entire distal-projecting portion of the sclerotized process is longer than the proximal-attached portion (agreeing with our observations). Only figure 168 in Szczytko & Stewart (1979) provides an accurate view of the "arms of the apical fork" length, illustrating both as half the length of the proximal-attached "base" portion (0.5 times shorter than our observations), and subequal to the "base" of the distal-projecting portion of the sclerotized process (agreeing with our observations). Couplet 20 provides another sclerotized process length character "dorsal arms of sclerotized aedeagal process not extending beyond length of base…(figs. 165C & 168)". Couplet 20 describes the lengths as they are illustrated in fig. 168 (inconsistent with our observations), but then conflicts with fig. 165C because the dorsal arms (same as "arms of apical fork" above) extend beyond the length of the "base" or proximal-attached portion (agrees with our observations).

The current study addresses this uncertainty by providing updated terminology for the four regions of the *I. bifurcata* sclerotized process: **1**. base, proximal portion attached to aedeagal membrane, bifurcate posteriorly and apically recurved (Fig. 4a, 1); **2**. median arm, projecting ventrally from aedeagal membrane (Fig. 4a, 2); **3.** bifurcate arms, extending ventrally from median arm (Fig. 4a, 3); and **4**. short sharp subapical barb and slightly longer apical tine at apex of bifurcate arms (Fig. 4a, 4).

The total length of the *I. bifurcata* distal-projecting portion of the sclerotized process (median arm, bifurcate arms and apical tines) (Fig. 4a, 2+3+apical tine) is nearly 2 times the length of the proximal-attached base (Fig. 4a, 1); and the bifurcate arm + apical tine length (Fig. 4a, 3+apical tine) is subequal to median arm length (Fig. 4a, 2). Additionally, the length from the ventral barb apex to the apical tine apex (Fig. 4a, 4) ranged from subequal to less than the bifurcate arm length (Fig. 4a, 3).

Additional Material Examined. CALIFORNIA, Shasta Co., Hat Creek, Hwy 44, 3 mi (4.8 km) SW Old Station, 16/VII/2011, D.R. Givens, ♂, ♀ (CSUC); Siskiyou Co., McCloud River, Hwy 89 Lower Falls Picnic Area 5.5 mi (8.8 km) E McCloud, 41.2402°N, 122.02441°W, 23/V/2013, J.B. Sandberg, B.C. Kondratieff, 1♂ (JBSC).



Figs. 5-6. Adult male characters of *Isoperla denningi*, San Mateo Cr., San Diego Co., CA, and *I. fulva*, Sand Cr., Larimer Co., CO & Pole Cr., Juab Co., UT, 32-50x. Fig. 5a. *I. denningi* aedeagus, lateral; sclerotized process (arrow & inset-lateral view). Lobes A-B: posterobasal, C: posteroapical, D: dorsolateral pair. Fig. 5b. Aedeagus, ventral; sclerotized process (arrow & inset-posterior view). Fig. 5c. Paraprocts (arrow). Fig. 5d. Vesicle. Fig. 6a. *I. fulva* aedeagus, lateral; sclerotized process (left white arrow & inset-lateral view); spinule patch (right white arrow & inset); paraprocts (inset-black arrow). Lobes A: posterior, B: dorsal, C: anterior. Fig. 6b. Aedeagus, ventral; sclerotized process (arrow & inset-posterior view). Fig. 6c. Aedeagus, dorsal; sclerotized process (black arrow); spinule patch (white arrow). Fig. 6d. Vesicle.

Isoperla denningi **Jewett**
(Figs. 5a-d)

Isoperla denningi Jewett 1955. Holotype ♂, California, Los Angeles County, 4 mi W Tanbark Flat.

Male. Aedeagus: sclerotized posterior process present; body with two posterobasal lobes, one large posteroapical lobe, and one dorsolateral pair of rounded lobes (Fig. 5a); sclerotized process length < 0.5 mm, recurved and rod-like, apex clavate in lateral view (Fig. 5a), bifurcate in posterior view, lateral apices short and rounded (Fig. 5b), and width of expanded apicolateral lobes 0.09-0.10 mm. Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to blunt apices (Fig. 5c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 5d).

Isoperla denningi is common in southwestern California, from Santa Barbara County south to San Diego County and occasionally coexists with *I. acula*, *I. adunca* and *I. mormona* (Sandberg 2011b). It is most similar to the species in the *I. sordida* complex, specifically *I. sordida* Banks 1906 (Table 1), with discernible differences in aedeagal characters. Both species have four aedeagal lobes in lateral view, however *I. denningi* has a pair of dorsal lobes and *I. sordida* has only one. The sclerotized processes are somewhat similar; both are slightly bifurcate with short rounded apices. The difference is the plane in which these apices lie: for *I. sordida*, the apical plane is perpendicular to the body of the process, and for *I. denningi*, the apical plane is parallel with the sclerotized process body. Additionally, the widths of the bifurcate apices differ: 0.09-1.0 mm for *I. denningi* and 0.18-0.20 mm for *I. sordida*.

Additional Material Examined. CALIFORNIA, Riverside Co., San Juan Creek, 0.4 mi (0.6 km) N Lion Canyon Creek, 19/V/2011, larvae (ABLC); San Diego Co., Devils Canyon Creek, above San Mateo Canyon Creek, 16/V/2011, larvae (ABLC); King Creek, 1.1 mi (1.77 km) below Grove Drive, 30/V/2012, larvae (ABLC); Santa Ysebel Creek, 2 mi (3.2 km) S Dan Price Creek, 29/V/2011, larvae (ABLC); Juaquapin Creek, above Sweetwater River, 01/VI/2011, larvae (ABLC).

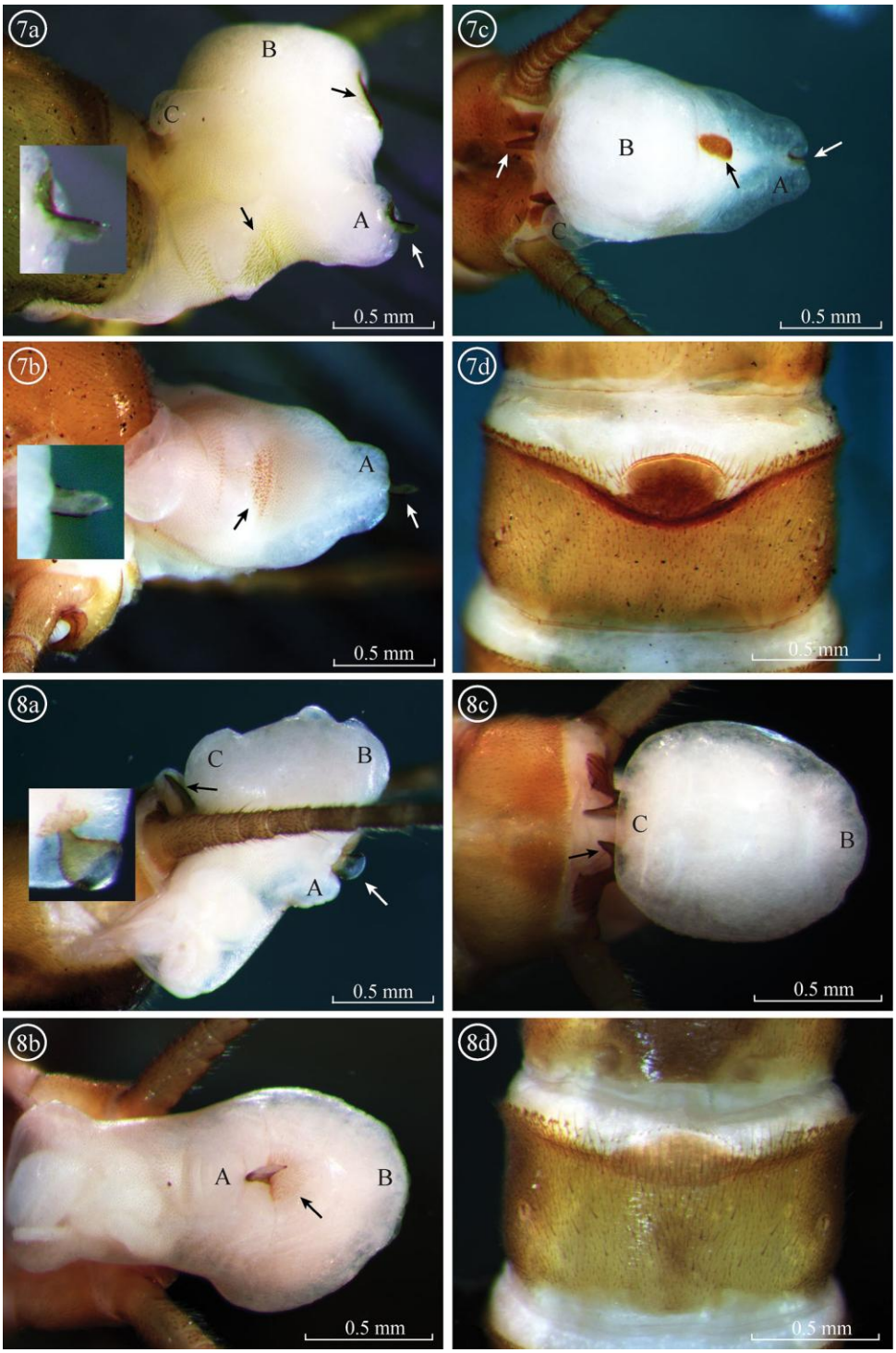
Isoperla fulva **Claassen**
(Figs. 6a-d, 20b)

Isoperla fulva Claassen 1937. Holotype ♂, Utah, Logan River.

Male. Aedeagus: sclerotized posterior process present; body with one posterior lobe, one small dorsal lobe, and one large anterior lobe (Fig. 6a); one small bulbous patch of spinulae above sclerotized process (Figs. 6a-c); sclerotized process length approaching 0.5 mm when fully extended, blade-like in lateral view (Fig. 6a), distal margin expanded and slightly membranous in posterior view (Fig. 6b), and narrow proximal portion of sclerotized process sometimes extended past posterior aedeagal membrane (Fig. 6a). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to blunt apices (Fig. 6a). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 6d).

Isoperla fulva is most similar to the two other *I. marmorata* complex species, *I. marmorata* and *I. roguensis*. These species differ in paraproct shape and aedeagal characters. The paraprocts taper abruptly to blunt apices in *I. fulva*, taper gradually to blunt apices in *I. marmorata*, and taper abruptly to tiny sharp apices in *I. roguensis* (Table 1). The distal margin of blade-like sclerotized processes is thin in *I. marmorata*, expanded in *I. fulva* and expanded and variably-shaped in *I. roguensis*.

The aedeagus of this species was described with an additional pair of long narrow tubular lobes extending from the base of the anterodorsal lobe (Szczytko & Stewart 1979, fig. 138C). When using the live eversion method, these processes remain inverted (Fig. 6a); however two small areas in inverted membrane are present on anterior lobe C of this study (not discernible in Fig. 6a). The live everted aedeagus was cleared in KOH, which



Figs. 7-8. Adult male characters of *Isoperla laucki*, Dragsaw Spring, Humboldt Co., CA, and *I. marmorata*, Big Chico Cr., Tehama Co., CA, 32-40x. Fig. 7a. *I. laucki* aedeagus, lateral; sclerotized process (white arrow & inset-lateral view); posteroapical and posterobasal spinule patches (black arrows). Lobes A: posterior, B: dorsal, C: anterolateral pair. Fig. 7b. Aedeagus, ventral; sclerotized process (white arrow & inset-dorsal view); posterobasal spinule patch (black arrow). Fig. 7c. Paraprocts (left white arrow); sclerotized process (right white arrow); posteroapical spinule patch (black arrow). Fig. 7d. Vesicle. Fig. 8a. *I. marmorata* aedeagus, lateral; sclerotized process (white arrow & inset-lateral view); paraprocts (black arrow). Lobes A: posterior, B: dorsal, C: anterior. Fig. 8b. Aedeagus, posterior; spinule patch & sclerotized process (black arrow). Fig. 8c. Paraprocts (arrow). Fig. 8d. Vesicle.

allowed observation of an inverted pair of tube-like processes within the aedeagus, and openings along the anteroapical margin (Fig. 20b). The small dorsal lobe B (Figs. 6a & c) in the current study possesses a pair of minute, closely placed holes from which seminal fluid streamed after live eversion and fixing. These dorsal aedeagal openings require further study before their function can be determined.

Isoperla fulva is putatively known from California based on three males and one female (El Dorado and Modoc counties - Jewett 1960) and Plumas County (Szczytko & Stewart 1979) collected in the 1940's and 1950's. No recent material (everted males) from California compares well with the Colorado and Utah specimens examined for this study, and the California *I. fulva* records were determined before the description of *I. roguensis*. The El Dorado County male was likely collected from Weber Creek, south of Camino, 10 miles (16 km) north of Placerville, where Sandberg (2011b) collected *I. marmorata* and *I. mormona*.

Additional Material Examined. COLORADO, Larimer Co., Sand Creek, Ruby Wash, Red Mountain Open Space, 24/V/2012, B.C. Kondratieff & D. Givens, 5♂, 2♀ (CSUC); 17/VI/2012, B.C. Kondratieff & R. Stokes, 10♂, 3♀ (CSUC). OREGON, Harney Co., Trout Creek, Whitehorse Ranch Rd 18 mi (29 km) SE Fields, 42.17439°N, 118.43199°W, 20-21/V/2013, J.B. Sandberg, B.C. Kondratieff, 2♂, 1♀ (JBSC); Union Co., Grande Ronde River, Hwy 244, Hilgard Junction State Park (Hwy 84), 45.34323°N, 118.24013°W, 22/V/2013, J.B. Sandberg, B.C. Kondratieff, 2♂, 3♀ (JBSC). UTAH, Juab Co., Pole Creek, FR016 below confluence Pole Canyon, 14/VI/2012, B.C. Kondratieff & R.W. Baumann, 10♂, 23♀ (CSUC); Salt Creek, Ponderosa Campground, 14/VI/2012, B.C. Kondratieff & R.W. Baumann, 2♂, 2♀ (CSUC); Utah Co., Nebo Creek, FR405, 13/VI/2012, B.C. Kondratieff & R.W. Baumann, 1♂, 8♀ (CSUC).

Isoperla laucki Baumann & Lee
(Figs. 7a-d)

Isoperla laucki Baumann & Lee 2009. Holotype ♂, California, Humboldt County, Dragsaw Spring @ Rd 13N01.

Male. Aedeagus: sclerotized posterior process present; body with one posterior lobe, one large dorsal lobe, and a pair of small anterolateral lobes (Fig. 7a); one posterobasal patch of spinulae scattered below the sclerotized process and a long narrow posteroapical spinule patch concentrated above the sclerotized process (Figs. 7 a-b); sclerotized process length < 0.5 mm, digitate, apex a blunt point, and capable of complete (Fig. 7a) to partial eversion (Fig. 7c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to blunt apices (Fig. 7c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 7d).

Isoperla laucki is most similar to *I. marmorata* (Table 1), with diagnostic differences in aedeagal spinule patch shape, location of sclerotized process, and sclerotized process shape. The spinules form an elliptical shaped patch distinctly separated from and placed above the insertion of the sclerotized process. The more rounded and in one case, bi-hemispherical shaped spinule patches of the *I. marmorata* complex are all placed above and adjacent to the insertion of the posterior sclerotized process. The *I. laucki* sclerotized process length is < 0.5 mm, has parallel lateral margins, and a bluntly rounded apex. The sclerotized processes of the *I. marmorata* complex are longer (approaching 0.5 mm), and have expanded dorsal and ventral margins forming a blade-like apex with variable distal margins.

The above male description, including live everted aedeagal characters, agrees with the previous description of the aedeagus based upon scanning electron microscope preparation (Baumann & Lee 2009, figs. 1-8). It was not noted in their methods if the live everted aedeagus was fixed in hot water. An unfixed aedeagus, after live eversion, will usually invert or deflate slightly, and might explain the slightly larger and expanded dorsal lobe in our study (Fig. 7a).

Additional Material Examined. CALIFORNIA, Humboldt Co., Unnamed tributary of Boise Creek, Hwy 299, 01/V/2011, J.B. Sandberg, B.C. Kondratieff, 1♀ (JBSC).

Isoperla marmorata (Needham & Claassen)
(Figs. 8a-d, 20c)

Clioperla marmorata Needham & Claassen 1925. Holotype ♀, Nevada.

Male. Aedeagus: sclerotized posterior process present; body with one small posterior lobe, one dorsal lobe and an anterior lobe (Fig. 8a); one small patch of spinulae concentrated on the inverted membrane above sclerotized process (Figs. 8a-b); sclerotized process approaching 0.5 mm when fully extended, blade-like in lateral view (Fig. 8a), distal margin thin in posterior view (Fig. 8b), and narrow proximal portion of sclerotized process usually inverted inside posterior aedeagal membrane. Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to long blunt apices (Fig. 8c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 8d).

The aedeagus of *I. marmorata* is more similar to *I. fulva* than to *I. roguensis* with similar numbers of spinule patches, patch shapes and positions. The *I. marmorata* aedeagus possesses two anteroapical small areas of inverted membrane which form the bases of the internal tube-like structures. Additionally, a pair of very small holes is present on the dorsal surface, usually on a minute lobe (not visible in Figs. 8a & 8c). The pairs of inverted membrane areas and minute holes occasionally have fixed streaming seminal fluid still attached.

The previous *I. marmorata* aedeagal description did not include extended apical tube-like lobes (Szczytko and Stewart 1979, fig. 123). After clearing the everted aedeagus in KOH, a pair of inverted tube-like processes were observed within the aedeagus and attached to the small inverted areas (openings) upon the anteroapical margin (Fig. 20c). It is possible that the previous description was based upon a live everted male that was not cleared.

Isoperla marmorata wing and body color varies significantly in California. Typically at lower elevations and into the foothills, abdominal coloration is mostly yellow (reddish-yellow in life) and hindwing anal areas are lightly tinted. An exception occurs at Butte Creek (near Chico) where both wings are completely tinted and males have a dark wide ventral band on the ninth sternum. At a higher elevation Big Chico Creek location (Tehama Co.), the abdomen is yellow with multiple brown markings and dark wings. An extreme adult phenotype of this species is found at Prairie Creek (Humboldt Co.) where the abdomen is almost completely brown and the wings nearly black (J.J. Lee, pers. com.).

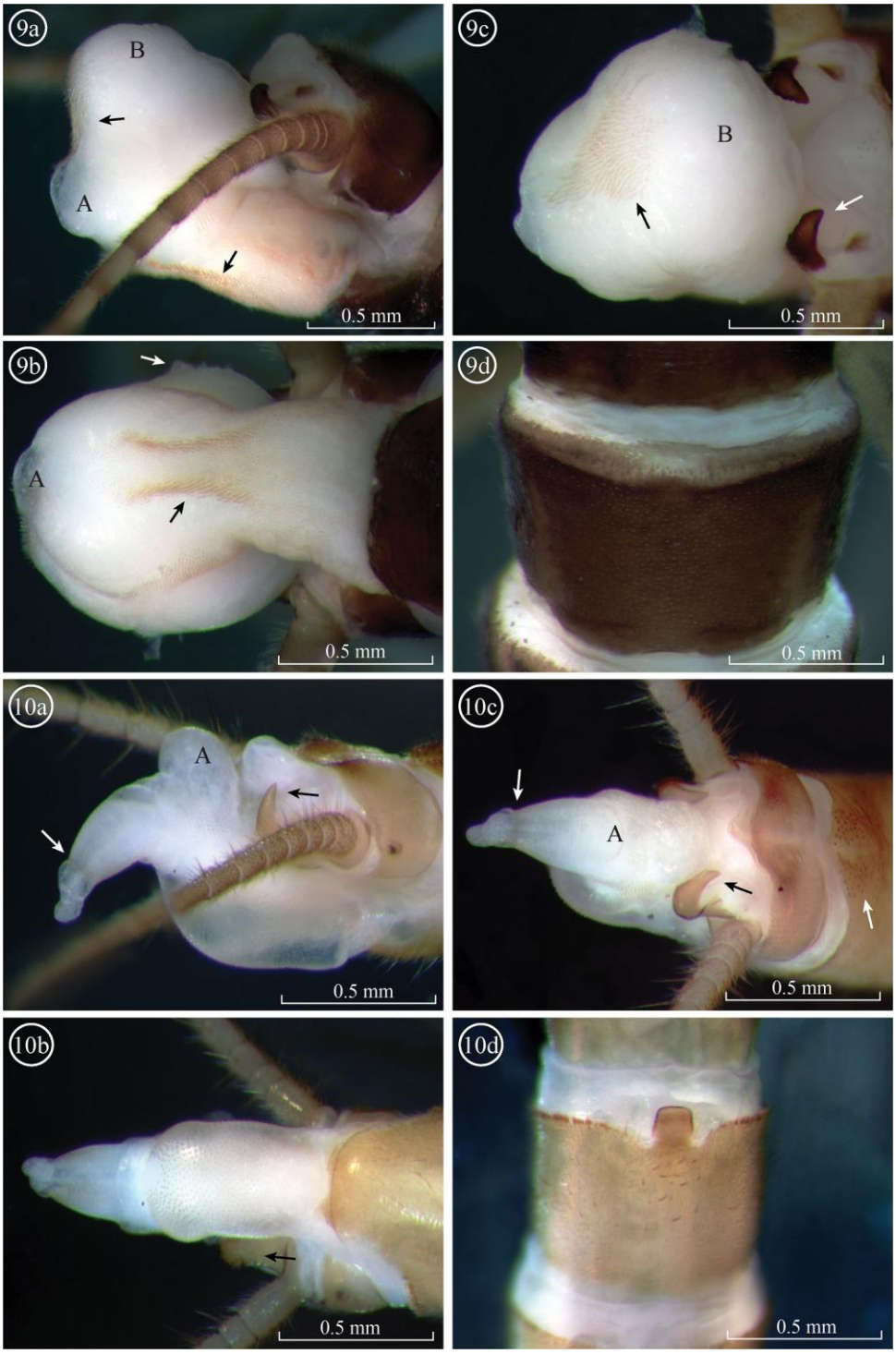
Additional Material Examined. CALIFORNIA, Siskiyou Co., McCloud River, Hwy 89 Lower Falls Picnic Area 5.5 (8.8 km) mi E McCloud, 41.2402°N, 122.02441°W, 23/V/2013, J.B. Sandberg, B.C. Kondratieff, 3♂, 1♀ (JBSC). OREGON, Lake Co., Deep Creek, Hwy 140, 5.5 mi (8.8 km) E Adel, 42.18564°N, 119.99512°W, 20/V/2013, J.B. Sandberg, B.C. Kondratieff, 4♂, 2♀ (JBSC).

Isoperla miwok Bottorff & Szczytko
(Figs. 9a-d, 20d)

Isoperla miwok Bottorff & Szczytko 1990. Holotype ♂, California, El Dorado County, Indian Creek, 3.3 km NE Michigan Bar Bridge.

Male. Aedeagus: sclerotized posterior process absent; body with one small posterior lobe, one large dorsal lobe and a pair of small pointed lobes on apicolateral margins (Fig. 9a-b); a pair of long curved patches of spinulae on posteroventral surface (Fig. 9b), and a broad patch of spinules on the posteroapical surface (Figs. 9a-c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to blunt apices (Fig. 9c). Vesicle: lobe barely perceptible, vestigial when present, widest at base with broadly rounded apex (Fig. 9d).

Isoperla miwok is most similar to the other species included in the *I. sobria* complex based on the absence of an aedeagal posterior sclerotized process, and



Figs. 9-10. Adult male characters of *Isoperla miwok*, Campbell Cr., Butte Co., CA and *I. mormona*, Big Chico Cr., Butte Co., CA, 40-50x. Fig. 9a. *I. miwok* aedeagus, lateral; posteroventral pair and posteroapical spinule patches (arrows). Lobes A: posterior, B: dorsal. Fig. 9b. Aedeagus, ventral; posteroventral pair of spinule patches (black arrow), small pointed apicolateral lobe (white arrow). Fig. 9c. Paraprocts (white arrow); posteroapical spinule patch (black arrow). Fig. 9d. Vesicle. Fig. 10a. *I. mormona* aedeagus, lateral; paraproct (black arrow); fine dorsoapical spinulae (white arrow). Lobe A-dorsoanterior. Fig. 10b. Aedeagus, ventral; paraproct base (arrow). Fig. 10c. Paraprocts (black arrow); fine dorsoapical spinulae (left white arrow); abdominal spinulae (right white arrow). Fig. 10d. Vesicle.

presence of stout spinules arranged in variable patches (Table 1). It is distinctive among the western Nearctic species in possessing a double band of stout spinulae on the aedeagal posterobasal margin.

The current study aedeagal description conforms to the previous description. However, the live everted and fixed aedeagus lacks the single extended tube-like lobe on the anteroapical margin (Bottorff et al. 1990, fig. 4). The anterior margin in this study possesses at least one anteromedian pair of inverted membrane areas (openings) which differs from the original description. A second smaller and more apical pair is also present. Clearing the everted and fixed aedeagus in KOH allowed observation of the anteroapical and anteromedian inverted processes inside the aedeagal body (Fig. 20d, dorsal aspect providing the best view).

Isoperla mormona Banks
(Figs. 10a-d)

Isoperla mormona Banks 1920. Holotype ♀, Utah, Utah County, Vinyard.

Male. Aedeagus: sclerotized posterior process absent; body a long recurved tube with one small dorsoanterior lobe, tapering to a multi-lobed apex (Figs. 10a-b); a thin light dorsoapical band of fine spinulae concentrated somewhat above bi-lobed tip (Figs. 10a-b). Mesoposterior area of ninth tergum with bipartite patches of stout dark spinulae and long fine scattered setae, tenth tergum without spinulae (Fig. 10c). Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to blunt apices (Fig. 10c). Vesicle: trapezoid shaped, length subequal to width, constricted near base with tapered and straight lateral margins (base wider than apex), apex truncate (Fig. 10d).

Isoperla mormona is most similar to *I. acula* and *I. quinquepunctata* (Table 1). See comments under *I. acula*.

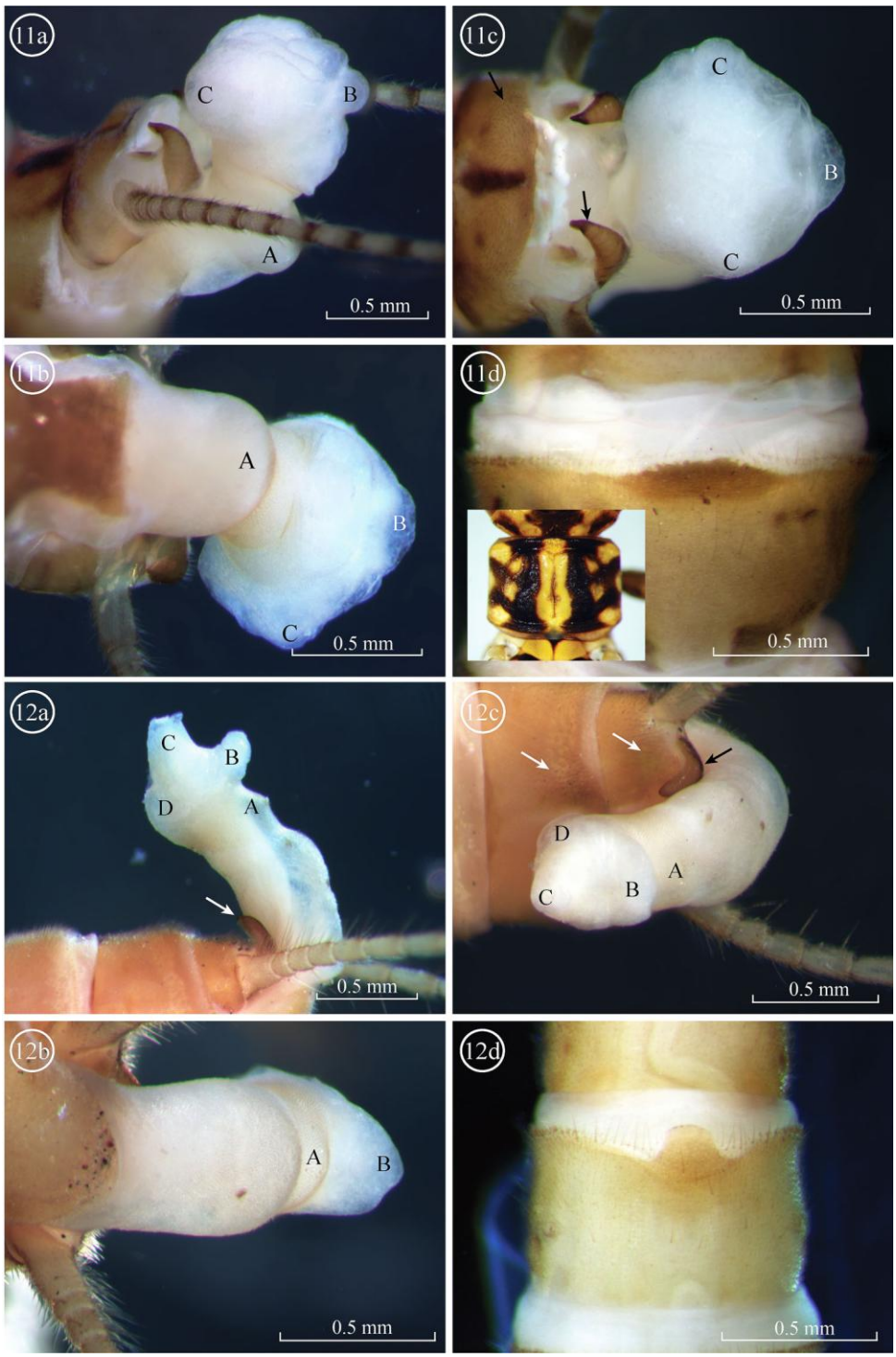
Additional Material Examined. CALIFORNIA, Inyo Co., Rawson Creek, 1.1 mi (1.8 km) above Gerkin Rd, ~ 7.5 mi (12.1 km) S Bishop (Hwy 395), 37.28640°N, 118.40420°W, 25/VII/2012, larvae (ABLC). San Diego Co., Santa Ysebel Creek, 2 mi (3.2 km) S Dan Price Creek, 29/V/2011, larvae (ABLC). OREGON, Harney Co., Trout Creek, NFD 395 Rd 4.25 mi (6.8 km) E Idlewild CG (Hwy 395), 43.80484°N, 118.91082°W, 21/V/2013, J.B. Sandberg, B.C. Kondratieff, 4 larva; Klamath Co., Sprague River, Hwy 140 unnamed access 4.74 mi (7.6 km) E Beatty, 42.44096°N, 121.18719°W, 19/V/2013, J.B. Sandberg, B.C. Kondratieff, 1♂ (JBSC).

Isoperla pinta Frison
(Figs. 11a-d)

Isoperla pinta Frison 1937. Holotype ♂, Oregon, Curry County, Floras Creek.

Male. Aedeagus: sclerotized posterior process absent; body with one posterobasal lobe, one small posteroapical lobe, and a pair of anterolateral lobes (Fig. 11a); Mesoposterior area of ninth tergum with bipartite patches of long fine light spinulae mixed with patches of long clear setae (best viewed from lateral angle). Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to blunt apices (Fig. 11c) apices usually secondarily barbed along ventral margin. Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 11d).

Isoperla pinta is very similar to *I. phalerata* Needham 1917, a species not known to occur in California. However, interestingly, Jewett (1954) designated the male allotype of *I. phalerata* from Union County, in northeastern Oregon, whereas the holotype locality of *I. pinta* is Curry County, in southwestern Oregon, bordering northern California (Frison 1937). *Isoperla phalerata* is presumably rarely collected and adults and larvae may be readily confused with *I. pinta*. At present, the most useful characters for separating adults of the two species include the pigment pattern of the head and pronotum (lighter *I. phalerata* vs. darker *I. pinta*) described in Szczytko & Stewart (1979, figs. 56 & 75); and variable cross veins between radial sector and M vein of forewings (one for *I. pinta* vs. more than one for *I. phalerata*) described in Smith (1917, fig. 65),



Figs. 11-12. Adult male characters of *Isoperla pinta*, Butte Cr., Butte Co., CA and *I. quinquepunctata*, Yuba R., Yuba Co., CA & Nehalem R., Clatsop Co., OR, 32-50x. Fig. 11a. *I. pinta* aedeagus, lateral. Lobes A: posterobasal, B: posteroapical lobe, C: anterolateral pair. Fig. 11b. Aedeagus, ventral. Fig. 11c. Paraprocts (arrow). Fig. 11d. Vesicle; prothoracic pigment pattern (inset-dorsal view). Fig. 12a. *I. quinquepunctata* aedeagus, lateral. Lobes A: posterobasal, B: posteroapical , C: dorsal, D: anterior. Fig. 12b. Aedeagus, ventral. Fig. 12c. Paraprocts (black arrow); abdominal spinules (white arrows). Fig. 12d. Vesicle.

Szczytko & Stewart (1979, fig. 60), and Béthoux (2005, fig. 12). Both species lack a sclerotized aedeagal process, distinct aedeagal spinule patches, and possess wide and short lobe-like vesicles. Dissimilar to the *I. pinta* continuous tergal spinule band pattern described previously (Szczytko & Stewart 1979, fig. 78); males observed in this study possess bipartite patches of fine light spinulae mixed with long clear setae. This generally matches the patch shape previously described for *I. phalerata* (Szczytko & Stewart 1979, fig. 59). Additionally, the ventral barb of the paraproct was vestigial in many specimens. When vestigial, its ventral margin curved interiorly, was in line with adjacent connective membrane instead of protruding ventrally, and was discernible only by darker pigment than the surrounding ventral paraproct.

Additional Material Examined. CALIFORNIA, Marin Co., Lagunitas Creek, 0.17 mi (0.3 km) N Jewell on Sir Francis Drake Blvd, N38.03917°, W122.74611°, 04/II/2013, L. Serpa, 1 Larva, (JBSC). OREGON, Klamath Co., Sprague River, Hwy 140 unnamed access 4.74 mi (7.6 km) E Beatty, 42.44096°N, 121.18719°W, 19/V/2013, J.B. Sandberg, B.C. Kondratieff, 10♂, 10♀ (JBSC).

Isoperla quinquepunctata (Banks)
(Figs. 12a-d)

Chloroperla 5-punctata Banks 1902. Holotype ♀, New Mexico, Las Vegas, Gallinas River.
Isoperla patricia Frison 1942. Holotype ♂, South Dakota, Lawrence County, Spearfish River, Spearfish.

Male. Aedeagus: sclerotized posterior process absent; body of aedeagus with a small posteromedian lobe covered with minute spinulae, one posteroapical lobe, one dorsal lobe, and an anterior lobe (Fig. 12a). Posterolateral margin of ninth and tenth terga with patches of long stout setae, fewer and smaller on tergum ten (Fig. 12c). Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to blunt apices (Fig. 12c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 12d), sometimes appears constricted along inner sclerotized lateral margins with wider and broadly rounded membranous outer lateral margins.

The live everted aedeagus agrees generally with the previous description (Szczytko & Stewart 1979, fig. 36). In this study, the small lobe A is covered with minute spinulae (Fig. 12a) vs. devoid of spinulae (Szczytko & Stewart 1979, fig. 36 D), and a truncated dorsal lobe C is present (Fig. 12a) vs. absent in Szczytko & Stewart (1979, fig. 36).

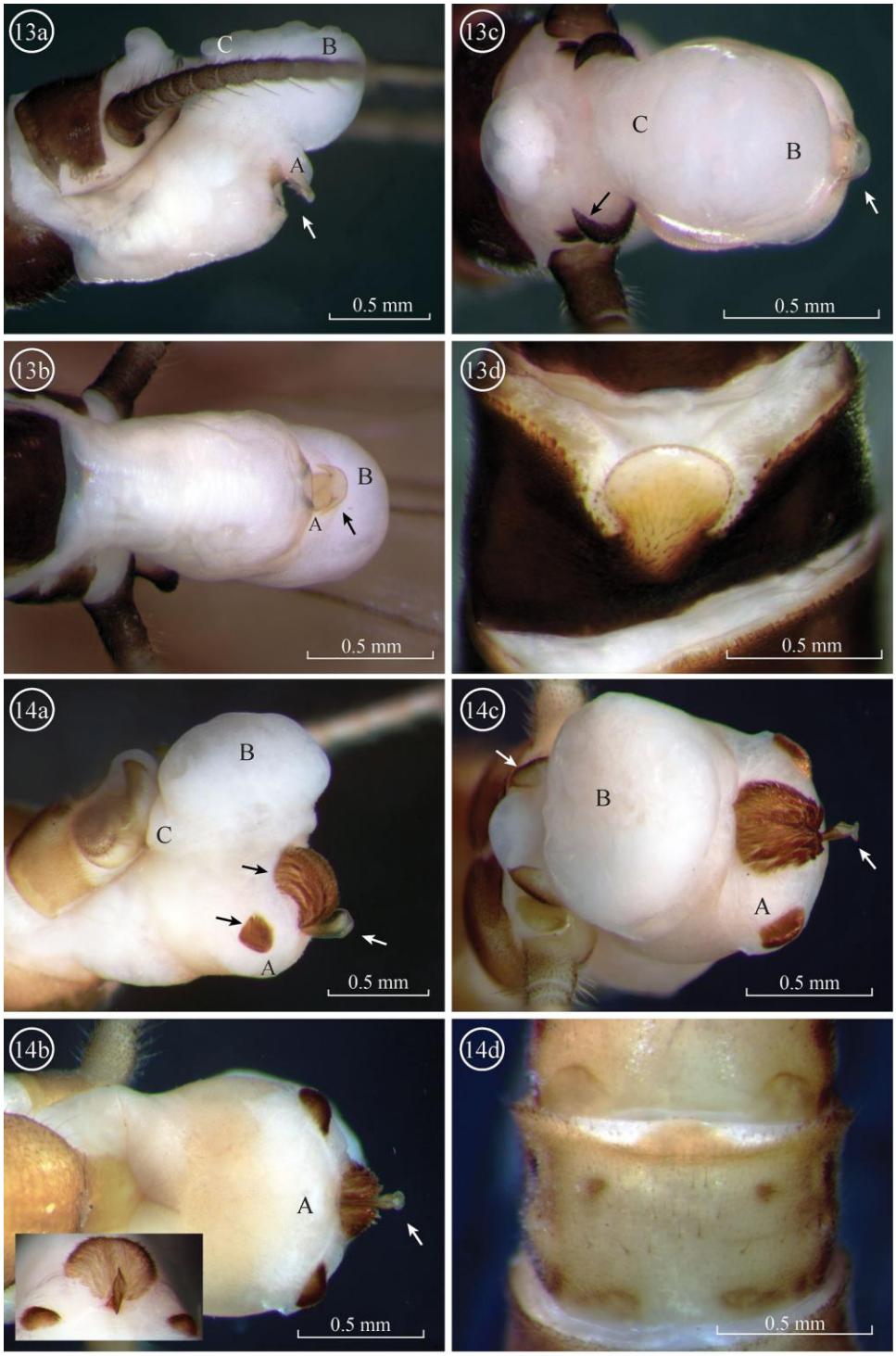
Isoperla quinquepunctata, a geographically widespread western Nearctic species (Szczytko & Stewart 1979) is most similar to *I. acula* and *I. mormona* (Table 1). See comments under *I. acula*.

Additional Material Examined. OREGON, Grant Co., Silvies River, Hwy 395, 0.6 mi (0.9 km) S Seneca, 44.12529°N, 118.97443°W, 21/V/2013, J.B. Sandberg, B.C. Kondratieff, 6♂, 3♀ (JBSC); Harney Co., Trout Creek, Whitehorse Ranch Rd 18 mi (28.9 km) SE Fields, 42.17439°N, 118.43199°W, 21/V/2013, J.B. Sandberg, B.C. Kondratieff, larvae (JBSC); Klamath Co., Sprague River, Hwy 140 unnamed access 4.74 mi (7.6 km) E Beatty, 42.44096°N, 121.18719°W, 19-20/V/2013, J.B. Sandberg, B.C. Kondratieff, 2♀ (JBSC); Lake Co., Crooked Creek, Hwy 395 at Chandler State Park 17 mi (27.3 km) N Lakeview, 42.41125°N, 120.29129°W, 20/V/2013, J.B. Sandberg, B.C. Kondratieff, 4♂, 3♀ (JBSC).

Isoperla rainiera Jewett
(Figs. 13a-d)

Isoperla rainiera Jewett 1954. Holotype ♂, Washington, Pierce County, Mount Rainier National Park.

Male. Aedeagus: sclerotized posterior process present; body of aedeagus with one small posterior lobe, one dorsal lobe, and one anterior lobe (Fig. 13a); sclerotized process length < 0.5 mm, recurved, crescent shaped, apex broadly rounded with two lateral sharp hook-like projections directed anteriorly (Figs. 13a-c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to long sharp apices



Figs. 13-14. Adult male characters of *Isoperla rainiera*, Tyee Spring, Skamania Co., WA and *I. roguensis*, Butte Cr., Butte Co., CA & Mad R., Humboldt Co., CA, 32-50x. Fig. 13a. *I. rainiera* aedeagus, lateral; sclerotized process (arrow). Lobes A: posterior, B: dorsal, C: anterior. Fig. 13b. Aedeagus, ventral; sclerotized process (arrow). Fig. 13c. Paraprocts (black arrow); sclerotized process (white arrow). Fig. 13d. Vesicle. Fig. 14a. *I. roguensis* aedeagus, lateral; sclerotized process (white arrow); spinule patches (black arrows). Lobes A: posterior, B: dorsal, C: anterior. Fig. 14b. Aedeagus, ventral (Mad R.); sclerotized process (arrow); inset-posterior view (Butte Cr). Fig. 14c. Paraprocts (left arrow); sclerotized process (right arrow). Fig. 14d. Vesicle.

(Fig. 13c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 13d).

Isoperla rainiera shares several characters with species of the *I. sordida* complex (Table 1). It differs from these species in paraproct shape and aedeagal characters. The paraprocts taper gradually to sharp apices and the apex of the sclerotized process is crescent shaped. This species is not known from California, recorded from Oregon and Washington (Szczytko & Stewart 1979).

Material Examined. WASHINGTON, Skamania Co., Tyee Spring, Meadow Creek Rd, 0.44 mi (0.7 km) N of NFD3065 & NFD30, 45.87568°N, 121.97095°W, 16/VI/2011, 2♂, 10♀ (JBSC).

Isoperla roguensis Szczytko & Stewart
(Figs. 14a-d, 20e)

Isoperla roguensis Szczytko & Stewart 1984. Holotype ♂, Oregon, Curry County, mouth of Rogue River.
Isoperla karuk Baumann & Lee 2009. Holotype ♂, California, Humboldt County, Klamath River @ junction of Aikens Creek. Syn. Sandberg, 2011b.

Male. Aedeagus: sclerotized posterior process present; body of aedeagus with one posterior lobe, one large dorsal lobe, and one anterior lobe (Fig. 14a); one bulbous and usually bi-hemispherical shaped patch of spinulae above sclerotized process and a small pair of spinule patches placed laterally (Figs. 14a-c); sclerotized process length approaching 0.5 mm, blade-like in lateral view (Fig. 14a), distal margin expanded and slightly membranous in posterior view (Fig. 14b), shape of distal expanded margin variable, and narrow proximal portion of sclerotized process usually inverted inside posterior aedeagal membrane. Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to tiny sharp apices (Fig. 14c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 14d).

Isoperla roguensis shares similar characters with the species of the *I. marmorata* complex (Table 1). See comments under *I. fulva*. Three distinct spinule patches distinguishes this species. Recently, Sandberg (2011b) placed *I. karuk* Baumann & Lee 2009 as a junior subjective synonym.

The previously described everted anterior tube-like lobes (Szczytko & Stewart 1984, fig. 55) remained inverted after live eversion, their positions indicated by a pair of small inverted areas of membrane (openings). After clearing in KOH, the internal tube-like processes were visible with openings along anteroapical margin (Fig. 20e, ventral aspect provided clearest view).

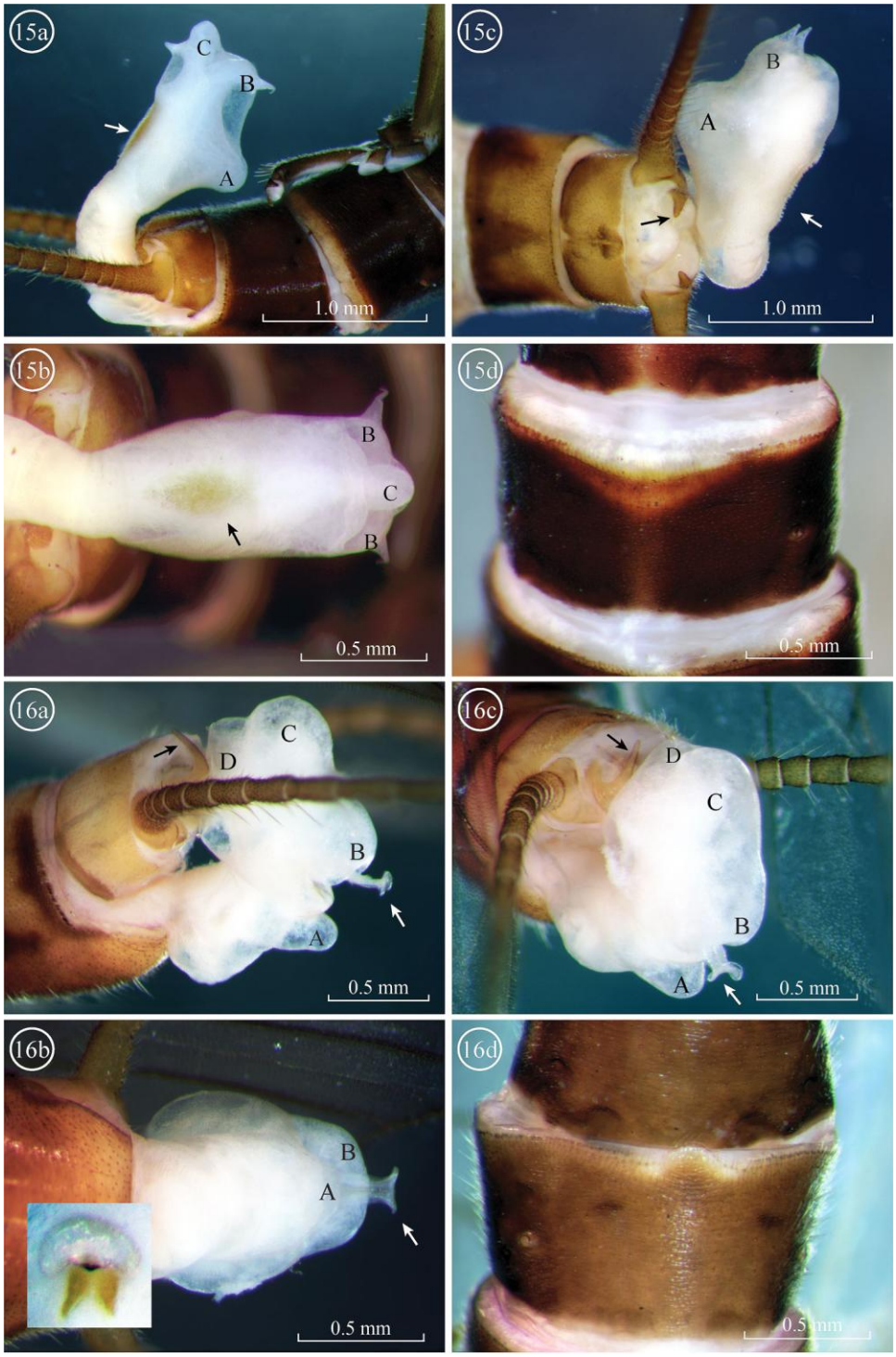
Additional Material Examined. CALIFORNIA, Plumas Co., MF Feather River, FR 12N61X access off Hwy 70, 10.5 mi (16.9 km) SE Quincy, 39.86453°N, 120.76138°W, 18/VI/2013, J.L. York, 1♂, 1♀ (JBSC); Jamison Creek, 1.6 mi (2.6 km) E Two Rivers exit off Hwy 70, 39.813°N, 120.6821°W, 19/VI/2013, J.L. York, 1♀ (JBSC).

Isoperla sobria (Hagen)
(Figs. 15a-d)

Perla sobria Hagen 1874. Holotype ♀, "Colorado mountains."
Perla ebria Hagen 1874. Holotype ♀, "Colorado mountains."
Isoperla sobria: Szczytko & Stewart 1979.

Male. Aedeagus: sclerotized posterior process absent; body of aedeagus typically with one anterior lobe and a pair of conical dorsal lobes (Figs. 15a-c); in one male collected in copula, a small posteroapical lobe was present (Figs. 15a-b); one long median patch of spinulae along posterior margin (Figs. 15a-c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering abruptly to blunt points (Fig. 15c). Vesicle: lobe barely perceptible, at best represented by an area of lighter pigment (Fig. 15d).

Isoperla sobria is most similar to *I. miwok* (Table 1), with both included in the *I. sobria* complex (Bottorff et al. 1990). They differ most in the shape of the aedeagal spinule patch. In *I. sobria*, there is only one



Figs. 15-16. Adult male characters of *Isoperla sobria*, Tyee Spring, Skamania Co., WA and *I. sordida*, Cold Water Cr., Mono Co., CA, 25-40x. Fig. 15a. *I. sobria* aedeagus, lateral (Tyee Sp., in copula); spinule patch (arrow). Lobes A: anterior, B: dorsal pair, C: posteroapical (aberrant). Fig. 15b. Aedeagus, posterior; spinule patch (arrow). Fig. 15c. Paraprocts (black arrow), Lk. Davis-Corral Sp.; spinulae patch, lateral (white arrow); dorsal pair of lobes in typical position. Fig. 15d. Vesicle. Fig. 16a. *I. sordida* aedeagus, lateral; sclerotized process (white arrow); paraproct (black arrow). Lobes A: posteroventral, B: posteromedian, C: dorsal, D: anterior. Fig. 16b. Aedeagus ventral; sclerotized process (arrow & inset-posterior view). Fig. 16c. Paraprocts (black arrow); sclerotized process (white arrow). Fig. 16d. Vesicle.

median patch on the posterobasal margin; in *I. miwok*, there is a posteroapical and a posterobasal patch, and the latter is concentrated into two nearly parallel bands. *Isoperla sobria* is distributed in higher elevation permanent streams in central to north-central California. *Isoperla miwok*, as with *I. acula* and *I. adunca*, is usually associated with small intermittent streams of the Sierra Nevada foothills in north-central California, with one unconfirmed Lake County, Coastal Range location (Sandberg 2011b).

Isoperla sordida Banks
(Figs. 16a-d)

Isoperla sordida Banks 1906. Holotype ♂, California, Los Angeles.

Male. Aedeagus: sclerotized posterior process present; body of aedeagus with two posterior lobes, one dorsal lobe, and one anterior lobe (Fig. 16 a); sclerotized process length approaching 0.5 mm, partially recurved and rod-like, apex expanded, flattened and projecting dorsally in lateral view (Figs. 16a), bifurcate subapically with two ventrally directed rounded lobes in posterior view (Fig. 16b inset), width of lobes 0.18-0.20 mm. Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to long blunt apices (Fig. 16c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 16d).

Isoperla sordida has been recently collected in two high elevation (above 1524 m), spring fed or snow melt eastern Sierra Nevada streams (Sandberg 2011b); and shares similar characters with other species from the *I. sordida* complex and *I. umpqua* (Table 1). It is most similar to *I. denningi*. See comments under *I. denningi*.

Isoperla tilasqua Szczytko & Stewart
(Figs. 17a-d, 20f)

Isoperla tilasqua Szczytko & Stewart 1979. Holotype ♂, Oregon, Benton County, Oak Creek.

Male. Aedeagus: sclerotized posterior process absent; body with two large posterior lobes and expanded apex, apex deeply inverted, with a pair of small conical lobes at apicolateral margins (Fig. 17a); one large patch of spinulae concentrated below posteromedian lobe (Fig. 17b), and a long thin patch along posteroapical margin (Fig. 17c). Abdominal terga 8-9, 9, 9-10: without stout spinulae or long stout setae. Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to first cercal segment, tapering abruptly to blunt apices (Fig. 17c). Vesicle: rounded lobe, widest at base with broadly rounded apical margin (Fig. 17d).

Isoperla tilasqua is not known from California, recorded from Oregon and Washington (Szczytko & Stewart 1979, Sandberg 2011b) and is most similar to *I. baumanni*. See comments under *I. baumanni*.

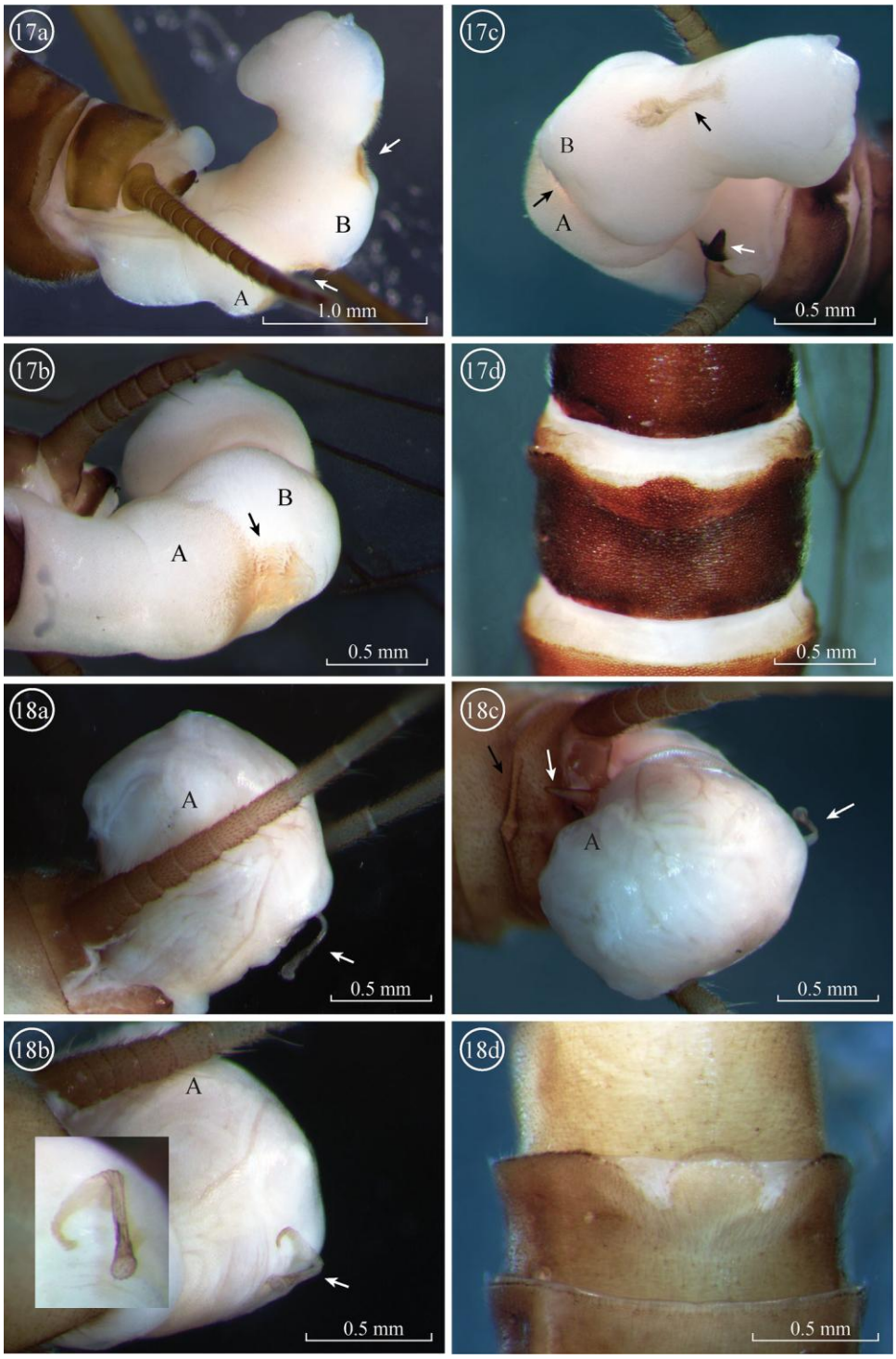
After live eversion, the extended tube-like lobes described in Szczytko & Stewart (1979, fig. 116) remained inverted, their locations could be identified by small inverted membrane areas (openings). After clearing in KOH, a pair of tube-like internal processes was discernible within the body of the aedeagus, with openings along the anteroapical margin (Fig. 20f).

Additional Material Examined. OREGON, Harney Co., Trout Creek, NFD 395 Rd 4.25 mi (6.8 km) E Idlewild CG (Hwy 395), 43.80484°N, 118.91082°W, 21/V/2013, J.B. Sandberg, B.C. Kondratieff, 4 Larvae, 2♂, 3♀ (reared) (JBSC); Umatilla Co., Camas Creek, Hwy 395 Ukiah-Dale Forest State Park 1.1 mi (1.8 km) S Hwy 244 intersec, 45.1241°N, 118.97251°W, 22/V/2013, J.B. Sandberg, B.C. Kondratieff, 2♂, 1♀ (JBSC).

Isoperla umpqua Szczytko & Stewart
(Figs. 18a-d)

Isoperla muir Szczytko & Stewart 2004. Nomen nudum.
Isoperla umpqua Szczytko & Stewart 2013. Holotype ♂, Oregon, Douglas County, Muir Creek, Hwy 230, downstream from bridge.

Male. Aedeagus: sclerotized posterior process present; body with one large dorsoanterior lobe (Fig. 18a); sclerotized process length approximately 0.5 mm,



Figs. 17-18. Adult male characters of *Isoperla tilasqua*, Meacham Cr., Umatilla Co., OR and *I. umpqua*, Muir Cr., Douglas Co., OR, 25-40x. Fig. 17a. *I. tilasqua* aedeagus, lateral; large basal spinule patch & thin apical patch (arrows). Lobes A-B: posterior. Fig. 17b. Aedeagus, posterior; large basal spinule patch (arrow). Fig. 17c. Paraprocts (white arrow); apical thin spinule patch (right arrow); large basal patch (left arrow). Fig. 17d. Vesicle. Fig. 18a. *I. umpqua* aedeagus, lateral; sclerotized process (arrow). Lobe A: dorsoanterior. Fig. 18b. Aedeagus, ventral; sclerotized process (arrow & inset-posterior view). Fig. 18c. Paraproct (left white arrow); sclerotized process (right white arrow); abdominal tergite 9 spinulae (black arrow). Fig. 18d. Vesicle.

recurved and rod-like, with parallel lateral margins, apex clavate, and distal margin rounded in lateral and posterior views (Figs. 18a-c). Mesoposterior area of eighth and ninth terga with bipartite patches of short stout spinulae and long fine scattered setae (Fig. 18c). Posterolateral margins of at least abdominal segment 8 with scale-like setae clustered in brushes of several setae. Paraprocts: curved dorsally, length if straightened subequal to combined first and second cercal segments, tapering gradually to long blunt apices (Fig. 18c). Vesicle: pedunculate, length subequal to width, constricted near base with curved lateral margins, wider and rounded at apex (Fig. 18d).

Based upon the presence of a sclerotized posterior process, absence of distinct aedeagal spinule patches, and pedunculate vesicle shape, *I. umpqua* is placed within the *I. sordida* complex (Table 1). It differs from all other *I. sordida* complex species by possessing short stout spinulae arranged in bipartite patches along mesoposterior margins of terga 8-9. The clavate sclerotized posterior process is most similar to *I. adunca*; however its length is approximately twice as long as *I. umpqua*. *Isoperla umpqua* is known only from Oregon, and similar to *I. baumanni*, is from a single location.

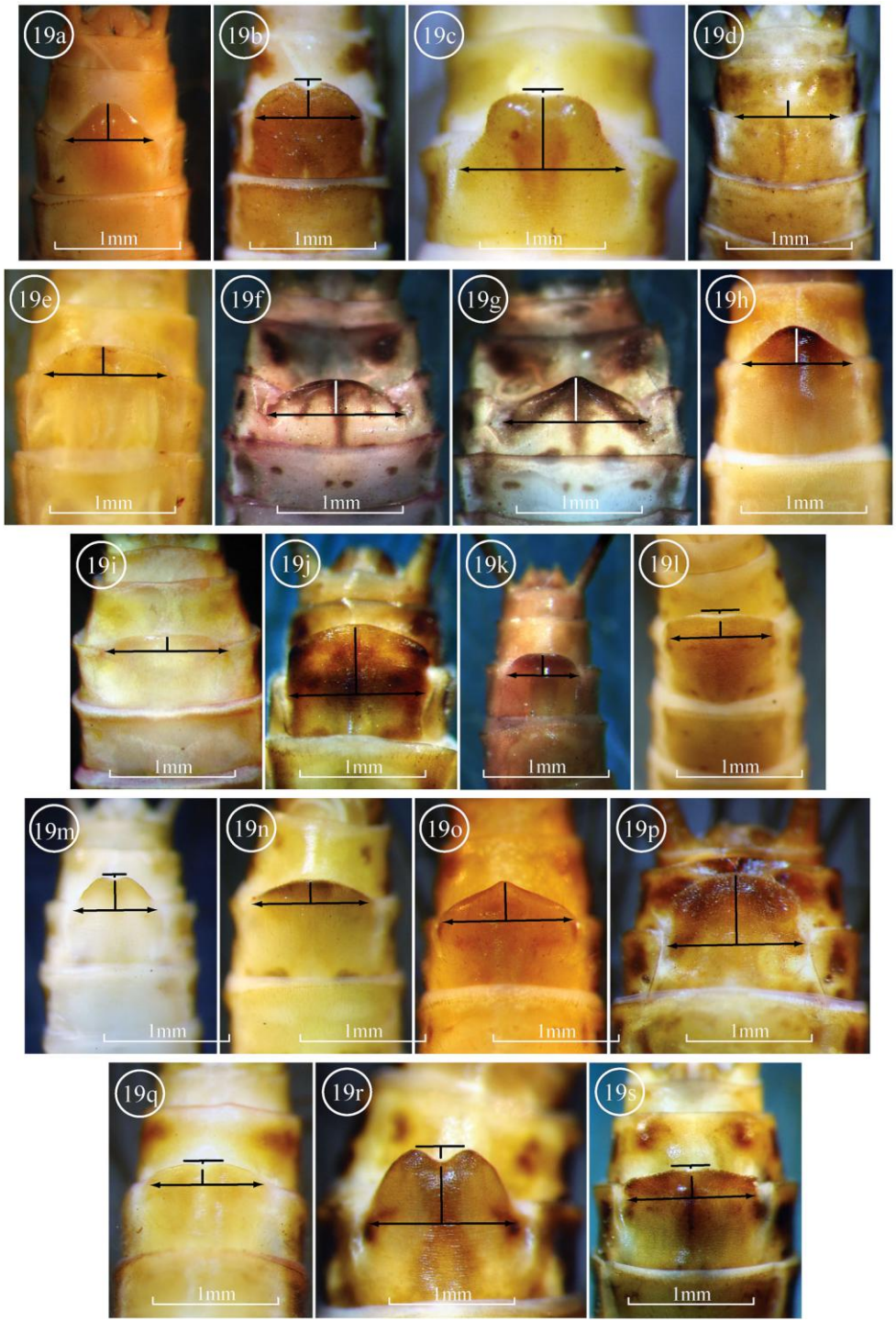
DISCUSSION

The six male characters primarily used to separate the 18 *Isoperla* species in this study (Table 1), and the finer details of the aedeagus and other characters, support the species complexes by Szczytko & Stewart (1979). None of the differences (except those resulting from two different eversion methods) between the current study and previous descriptions are significant and may all be attributed to intraspecific variations. Recently observed adult pigment differences between northern California populations of *I. marmorata* (Sandberg 2011b), and other slight morphological differences between *Isoperla* populations, may indicate the presence of cryptic species, or variation due to local environmental differences (ecophenotypes). The species limits in Nearctic *Isoperla* should be tested further by using scanning electron microscopy studies of minute aedeagal spinulae characters and molecular studies. The results from both should be compared with species limits from currently recognized morphological characters.

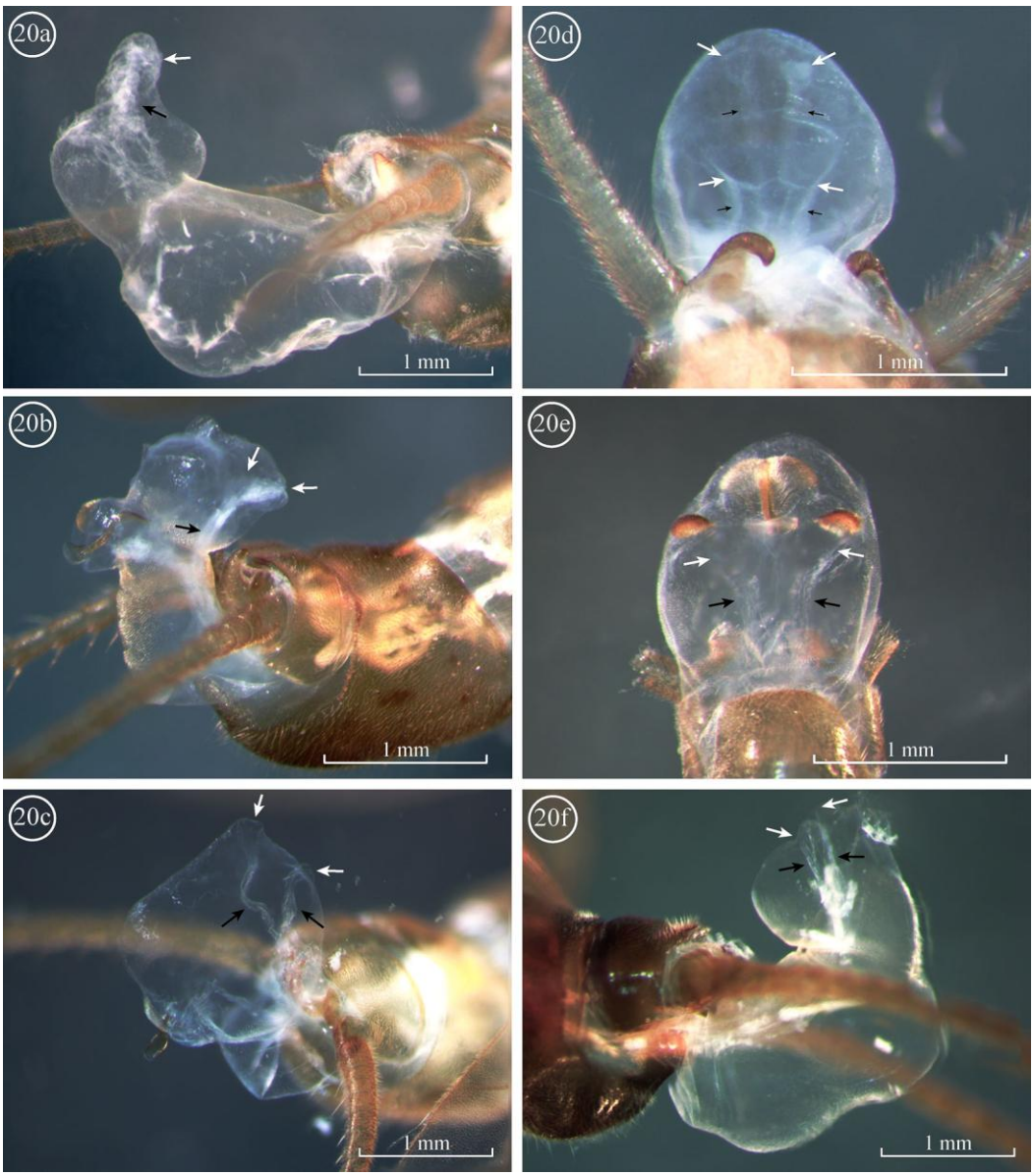
The laboratory eversion of the live male aedeagus performed under a dissecting microscope and fixed in near boiling water had variable results. Sandberg (2011b) stated that no two live males could be everted to the same extent. Variation of aedeagal eversions included lobe size and position, the amount of protrusion and direction of the sclerotized process from the aedeagus membrane, and overall size of the aedeagus. Caution is advised to users of the male species key; consider preparing a series of live males to increase the likelihood of full eversion.

The evenly spaced minute spinulae covering the aedeagal membrane were not included in the current study descriptions due to their minute size. Twenty-four western Nearctic *Isoperla* species have this character described and illustrated (Baumann & Lee 2009, Bottorff et al. 1990; Szczytko & Stewart 1979, 1984, 2002, 2004, 2013). It was not possible to completely document minute spinulae shape and size using cameras and a dissecting microscope. The use of minute spinulae characters will likely increase the precision of aedeagal descriptions, especially for those lacking sclerotized processes.

Six descriptions of the aedeagus differ when using the live eversion or the preserved eversion method (*I. baumanni*, *I. fulva*, *I. marmorata*, *I. miwok*, *I. roguensis*, and *I. tilasqua*). The preserved (in alcohol or ethanol) eversion method uses KOH to clear internal soft tissue prior to eversion. Heating the KOH along with mechanical eversion (Szczytko & Stewart 1979), presumably causes the additional eversion (or hyper-eversion) of normally internal, tube-like processes (Sandberg 2011b). Hyper extended tube-like processes were not present during copulation (based upon observations of preserved pairs in copula). The live aedeagus eversion method did not evert the internal tube-like processes, which remain inverted, and are located beneath small areas of inverted membrane on the surface. The different results from the two methods can be made comparable by clearing the live everted aedeagus in KOH and confirming the presence of internal tube-like processes (Fig 20a-f). Clearing with KOH after live eversion was only necessary in the key to positively separate two similar species, *I. baumanni* and *I. tilasqua*. The previous aedeagal description of *I. miwok* (Bottorff et al. 1990) is updated from



Figs. 19a-s. *Isoperla* subgenital plates, 50x. Horizontal arrows = subgenital plate width at base, vertical line (two lines when subgenital plate apex invaginated) = subgenital plate length, horizontal line = invagination width at apex. 19a. *I. acula*; 19b. *I. adunca*; 19c. *I. baumanni*; 19d. *I. bifurcata*; 19e. *I. denningi*; 19f. *I. fulva*, rounded; 19g. *I. fulva*, triangular; 19h. *I. laucki*; 19i. *I. marmorata*; 19j. *I. miwok*; 19k. *I. mormona*; 19l. *I. pinta*; 19m. *I. quinquepunctata*; 19n. *I. rainiera*; 19o. *I. roguensis*; 19p. *I. sobria*; 19q. *I. sordida*; 19r. *I. tilasqua*; 19s. *I. umpqua*.



Figs. 20a-f. The cleared aedeagus of six western Nearctic *Isoperla* species after live evertion; membranous opening of internal tube like process or apex (white arrows); tube like internal process (black arrows). 50x (20b, d & e, cropped and enlarged). 20a. *I. baumanni*, lateral view, partially everted; 20b. *I. fulva*, lateral view; 20c. *I. marmorata*, lateral view; 20d. *I. miwok*, dorsoapical view, tube like process openings along anteroapical margin; 20e. *I. roguensis*, ventral view, tube like process openings along anteroapical margin; 20f. *I. tilasqua*, lateral view.

possessing a single anteromedian extended tube-like inverted process to possessing two pair (Fig. 20d), and *I. marmorata* from lacking (Szczytko & Stewart 1979) to possessing an anteromedian pair of inverted tube-like processes (Fig. 20c).

The female subgenital plate shape (Figs. 19a-s) generally conforms to previous descriptions. Two species that did differ, *I. denningi* and *I. tilasqua*, may be due to variation of the subgenital plate throughout the range of these species, similar to *I. fulva*.

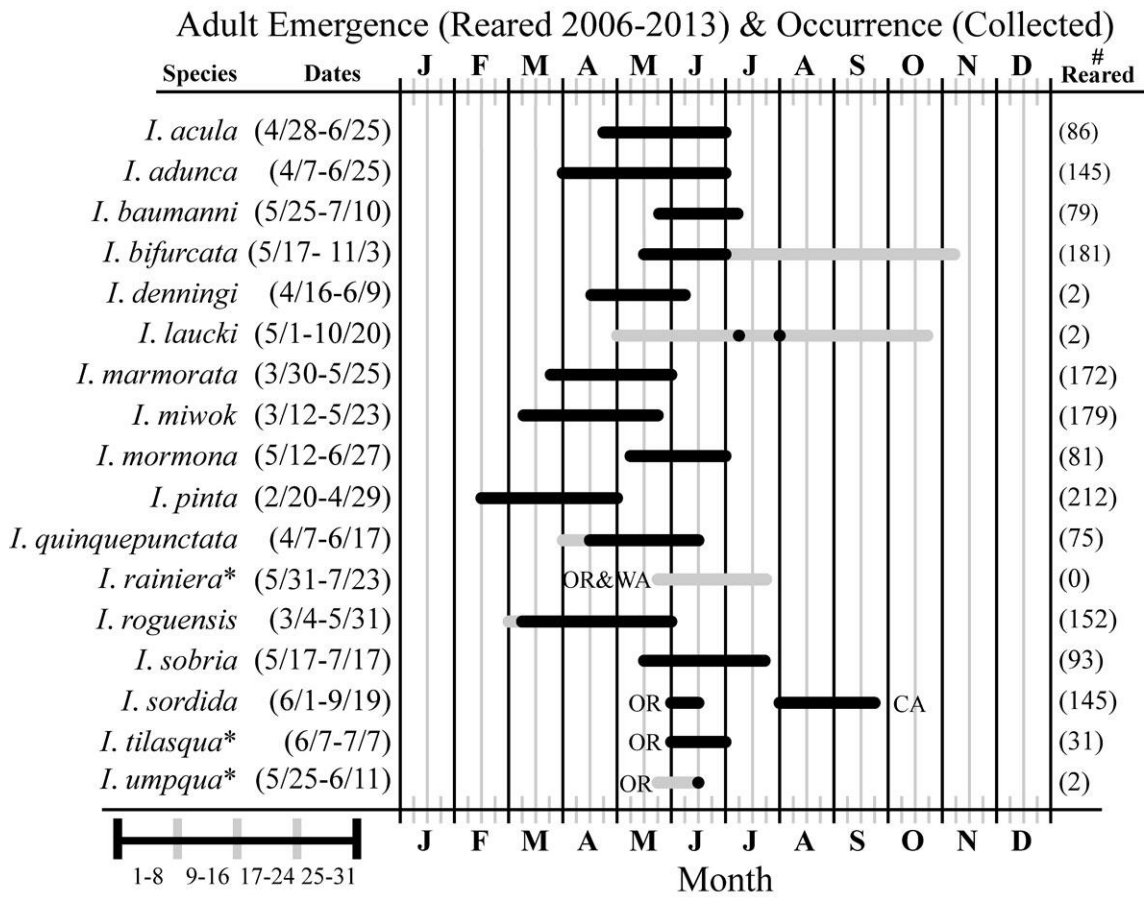


Fig. 21. *Isoperla* adult emergence phenology for 16 species reared from 2006-2013 and adult occurrences in the field for five species from California, Oregon, and Washington. Black horizontal bars indicate adult emergence, gray bars indicate field collections. Adult collections dates for *I. laucki*, *I. rainiera* and *I. umpqua*, were obtained from Baumann & Lee (2009) and Szczytko & Stewart (1979, 2004, 2013), respectively. Graduated bar below chart indicates range of dates for each month. Asterisk after species name indicates not known from California.

However, the previously described *I. denningi* female subgenital plate (Szczytko & Stewart 1979, fig. 180) is similar to *I. adunca* (Fig. 19b) and *I. quinquepunctata* (Fig. 19m), and the former is occasionally sympatric with *I. denningi*. The previously described *I. tilasqua* subgenital plate (Szczytko & Stewart 1979, fig. 117) had distinctly parallel lateral margins and a broadly rounded apical margin. In material examined during this study, the subgenital plate of *I. tilasqua* has nearly parallel lateral margins and an invaginated apical margin more similar to *I. gravitans* (Szczytko & Stewart 1979, fig. 111). Although the subgenital plate was typically rounded in *I. miwok*, one female reared from Campbell Creek tributary, Butte County, possessed a shallow median invagination along the apical margin.

Sixteen *Isoperla* species from California and Oregon were reared during this study. Figure 21 presents the adult emergence phenology under laboratory maintained 4.44-12.78°C water temperature. Additional dates (indicated by gray bars as adult occurrence) for *I. bifurcata*, *I. quinquepunctata*, and *I. roguensis* were from the authors collections. *Isoperla laucki*, *I. rainiera*, and *I. umpqua* collection dates were mostly from the literature (Baumann & Lee 2009, Szczytko & Stewart 1979, 2004, 2013). *Isoperla fulva* was not included in this chart.

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REFERENCES

Banks, N. 1902. Notes and descriptions of Perlidae. The Canadian Entomologist, 34:123-125.

Banks, N. 1906. New species of Perlidae. The Canadian Entomologist, 38:335-338.

Banks, N. 1920. New neuropteroid insects. Bulletin of the Museum of Comparative Zoology, 64:297-362.

Baumann, R.W. & J.J. Lee. 2009. Two interesting new species of *Isoperla* from northern California (Plecoptera: Perlodidae). Illiesia, 5:1-10.

Bottorff, R.L., S.W. Szczytko, & A.W. Knight. 1990. Descriptions of a new species and three incompletely known species of western Nearctic *Isoperla* (Plecoptera: Perlodidae). Proceedings of the Entomological Society of Washington, 92:286-303.

Claassen, P.W. 1937. New species of stoneflies (Plecoptera). The Canadian Entomologist, 69:79-82.

Frison, T.H. 1937. Studies of Nearctic aquatic insects. II. Descriptions of Plecoptera. Bulletin of the Illinois Natural History Survey, 21:78-99.

Frison, T.H. 1942. Studies of North American Plecoptera with special reference to the fauna of Illinois. Bulletin of the Illinois Natural History Survey, 22:235-355.

Hagen, H.A. 1874. Report on the Pseudo-Neuroptera and Neuroptera collected by Lieut. W.L. Carpenter in 1873 in Colorado. Pp. 571-606. *In* F.V. Hayden (editor). Annual Report of the United States Geological and Geographical Survey of the Territories, embracing Colorado, being a Report of Progress of the Exploration for the year 1873. Government Printing Office, Washington, D.C. 688 pp.

Haston, L. & J. Michaelsen. 1997. Spatial and temporal variability of southern California precipitation over the last 400 yr and relationships to atmospheric circulation patterns. Journal of Climate, 10:1836-1852.

Huntsman, B.O., R.W. Baumann, & B.C. Kondratieff. 1999. Stoneflies (Plecoptera) of the Black Hills of South Dakota and Wyoming, USA: Distribution and zoogeographic affinities. The Great Basin Naturalist, 59:1-17.

Jewett, S.G., Jr. 1954. New stoneflies (Plecoptera) from western North America. Journal of the Fisheries Research Board of Canada, 11:543-549.

Jewett, S.G., Jr. 1955. Notes and descriptions concerning western North American stoneflies (Plecoptera). The Wasmann Journal of Biology, 13:145-155.

Jewett, S.G., Jr. 1960. The stoneflies (Plecoptera) of California. Bulletin of the California Insect Survey, Volume 6, No. 6. University of California Press, Berkeley, California. 177pp.

Jewett, S.G., Jr. 1962. New stoneflies and records from the Pacific Coast of the United States. The Pan-Pacific Entomologist, 38:15-20.

Kondratieff, B.C. & R.W. Baumann. 2002. A review of the stoneflies of Colorado with description of a new species of *Capnia* (Plecoptera: Capniidae). Transactions of the American Entomological Society, 128:385-401.

Needham, J.G. & P.W. Claassen. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. Thomas Say Foundation, 397pp.

Sandberg, J.B. 2011a. Vibrational communication of *Isoperla* Banks from California and Oregon (Plecoptera: Perlodidae). Illiesia, 7:1-23.

Sandberg, J.B. 2011b. The *Isoperla* of California (Plecoptera: Perlodidae); larval descriptions and a key to 17 western Nearctic species. Illiesia, 7:202-258.

Sandberg, J.B. & K.W. Stewart. 2005. Holomorphology and systematics of the stonefly genus *Isogenoides* (Plecoptera: Perlodidae). Transactions of the American Entomological Society, 131:269-345.

Smith, L.W. 1917. Studies of North American Plecoptera (Pteronarcinae and Perlodini). Transactions of the American Entomological Society, 43:433-489.

Stewart, K.W. & M.W. Oswood. 2006. The stoneflies (Plecoptera) of Alaska and western Canada. The

Caddis Press. Columbus, Ohio. 325 pp.

Szczytko, S.W. & K.W. Stewart. 1979. The genus *Isoperla* (Plecoptera) of western North America; Holomorphology and systematics, and a new stonefly genus *Cascadoperla*. Memoirs of the American Entomological Society, 32:1-120.

Szczytko, S.W. & K.W. Stewart. 1984. Descriptions of *Calliperla* Banks, *Rickera* Jewett, and two new western Nearctic *Isoperla* species (Plecoptera: Perlodidae). Annals of the Entomological Society of America, 77:251-263.

Szczytko, S.W. & K.W. Stewart. 2002. New larval descriptions of 5 western Nearctic *Isoperla*: *I. decolorata*, *I. denningi*, *I. roguensis*, *I. katmaiensis* and *I. baumanni* and further descriptions of the male, female and ova of *I. decolorata* (Plecoptera: Isoperlinae). Transactions of the American Entomological Society, 128:1-22.

Szczytko, S.W. & K.W. Stewart. 2004. *Isoperla muir*, a new species of western Nearctic *Isoperla* and a new larval description of *Isoperla tilasqua* Szczytko and Stewart, (Plecoptera: Perlodidae). Transactions of the American Entomological Society, 130:233-243.

Szczytko, S.W. & K.W. Stewart. 2013. *Isoperla umpqua* a new species of western Nearctic stonefly. Illiesia, 9:28-33.

Zwick, P. 2000. Phylogenetic system and zoogeography of the Plecoptera. The Annual Review of Entomology, 45:709-746.

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