HOLOMORPHOLOGY AND DRUMMING BEHAVIOR OF WESTERN NEARCTIC *ISOPERLA* (PLECOPTERA)

DISSERTATION

Presented to the Graduate Council of the
North Texas State University in Partial
Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY

By

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Szczytko, Stanley W., Holomorphology and Drumming Behavior of Western Nearctic Isoperla (Plecoptera). Doctor of Philosophy (Biological Sciences), December, 1978, 306 pp., 2 tables, 32 plates, 261 figures, bibliography, 88 titles.

A neotype and allotype are designated for *Isoperla bilineata* (Say), and further descriptions of egg and nymph are given. The aedeagus has 2 dorsal, 1 anterolateral and 2 posterolateral lobes, an eversible posterodorsal sac and a long coiled anterodorsal membranous tube. The female subgenital plate is triangular and produced ca. 3/4 the length of the 9th sternum. The vagina bears a "Y"-shaped spinule pattern, and the seminal receptacle has 5-7 accessory receptacular glands, each lined with spinulae. The egg is oval, 0.39-0.42 mm width X 0.43-0.46 mm length, and the chorion is covered with large, regularly placed depressions. The collar is well developed, and micropyles are irregularly placed on a ridge below the polar ring. Nymphal laciniae have two apical teeth, and mandibles bear 4 main teeth and 2 subteeth. The nymphal proventriculus has a band of 23-26 rows of short, downward projecting spines.

The holomorphology of all life stages of 20 western Nearctic *Isoperla* and one *Cascadoperla* was studied over the 3-year period 1975-1978. One monotypic genus new to science, *Cascadoperla*, is described, and *Cascadoperla trictura* (Hoppe) designated as the type species. The nymph, adult male and female, and ova are described and illustrated. Three species new to science, *I. bifurcata*, *I. katmaiensis*, and *I. tilasqua*, were discovered. Detailed descriptions are given for both adult sexes and ova.

Two species are placed in synonymy. *I. patricia* Frison was found to be a synonym of *I. quinquepunctata* (Banks), and *I. ebria* (Hagen) was placed in synonymy with *I. sobria* (Hagen), based on a detailed comparative analysis of the ova from the type specimens.

The 21 species are arranged into 5 distinct complexes, and one unassigned species, primarily on the basis of male aedeagus and ova characters. The *I. quinquepunctata* complex is composed of *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, and *I. quinquepunctata* (Banks). *I. katmaiensis* is not assigned to a species group due to the unique unsculptured ova. The *I. phalerata* complex is composed of *I. phalerata* (Needham) and *I. pinta* Frison. The *I. ebria* consists of *I. ebria* (Hagen), *I. gravitans* (Needham and Claassen), and a new species *I. tilasqua.* The *I. marmorata* complex is composed of *I. fulva* Claassen and *I. marmorata* (Needham and Claassen). The *I. sordida* complex consists of *I. acula* Jewett, *I. adunca* Jewett, *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett,

I. sordida Banks, and a new species, I. bifurcata.

Six nymphal descriptions new to science are provided, with illustrations (nymph of I. sordida described from exuviae, no illustrations), including I. longiseta, I. marmorata, I. mormona, I. phalerata, I. rainiera, and Cascadoperla trictura.

Keys based on comparative morphology are provided for all known males, females, ova, and nymphs of Isoperla and Cascadoperla. Complete descriptions of ova with accompanying SEM photographs are provided for 20 species of Isoperla, and one species of Cascadoperla.

Drumming behavior of 4 species, I. fulva, I. quinquepunctata, I. mormona, and I. phalerata, representing 3 species complexes, were recorded. All exhibited substantive differences in the number of beats, signal duration, and inter-beat frequencies in both males and females. In all species, drumming was a simple, 2-way communication. Both monophasic and diaphasic signals were noted in the males. Inter-beat frequency was the most consistent parameter, and signal length exhibited the greatest variation in each species.

The morphological separation of Isoperla species complexes was further supported by the distinctiveness of signal parameters for each of the 3 complexes studied.

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PART I

CHAPTER I

INTRODUCTION AND METHODS

The genus *Isoperla*, now numbering ca. 125 Holarctic species, was proposed by Banks (1906), who designated *Isoperla bilineata* (Say) as the genotype. Say (1823) based his original description primarily on adult color patterns and included no illustrations of eggs, nymphs, or adult genitalia. The type locality was given as the Ohio River, near Cincinnati, but no type specimens were designated. Although other workers have provided additional descriptive information (Needham and Claassen 1925, Claassen 1931, Frison 1935), no neotype has been designated and no detailed analysis of external and internal genitalia, nymph, and egg have been made.

Reassignment of the genus to different families (Needham and Claassen 1925, Frison 1935, 1942), assignment of new species to the genus, and synonymy of other genera with *Isoperla* (*Clioperla* Needham and Claassen by Frison 1935; *Megahelus* Klapalek by Claassen 1940; *Suzukia* Okomoto by Ricker 1952; *Perliphanes*, *Occiperla*, *Nanoperla*, *Walshiola*, and *Perliola* Banks by Ricker 1962), without benefit of genotype specimens for comparisons have pointed up the need for designation of a neotype and allotype, and further study of the egg and nymph. This need and the usefulness of a revision of the genus *Isoperla* was expressed at the V International Symposium on Plecoptera in 1974 by both European and North American plecopterists.

The importance of internal adult genitalia, nymphal mouthparts, and eggs in Plecoptera study is becoming increasingly recognized. In this study I have utilized to a large extent a Model ISI Mini-SEM scanning electron microscope (International Scientific Instruments) for study of eggs and nymphal setal patterns and cerci. Aedeagi of preserved males were everted for study by the technique described by Szczytko and Stewart (1976); the aedeagus of one male from Illinois was fully everted at time of collection.

CHAPTER II

RESULTS AND DISCUSSION

Isoperla bilineata (Say)

Sialis bilineata: Say, 1823, Goodman's Western Quart. 2:165.

Perla picta: Walker, 1852, Perlides, 161.

Perla bilineata: Hagen, 1861, Syn. Neur. North Am., 30.

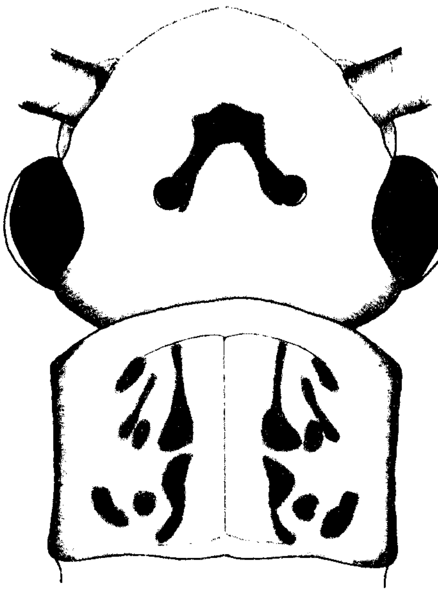
Chloroperla bilineata: Banks, 1892, Trans. Am. Entomol. Soc., 19:342.

Isoperla bilineata: Banks, 1906, Entomol. News, 17:175.

Isoperla transmarina: Claassen, 1940, Mem. Cornell Univ. Agric. Exp. Sta., 232:198.

Male.-- Macropterous. Body length 10.4-13.0 mm; length of forewings 13.1-14.6 mm. General body color light yellow; antennae and cerci lighter yellow. Cerci with long dorsal and ventral hair at posterior end of each segment; dorsal hairs continue for only 11 segments. Head as wide as prothorax; light yellow; ocellar triangle with dark inverted "V" connecting lateral ocelli with median ocellus (Fig. 1). Pronotum wider than long, with dark rugose markings contrasting with light yellow background (Fig. 1). Abdomen light yellow with faint traces of nymphal longitudinal stripes and rows of dots; abdominal terga and sterna covered with hairs (Fig. 2). Ventral lobe of 8th sternum

Plate I, Figs. 1-8. _I_. _bilineata_. 1. male adult head and pronotum. 2. male terminalia, dorsal aspect. 3. male terminalia lobe, vpll - ventral posterolateral lobe, all = anterolateral lobe, cmt - coiled membranous tube, pds - posterodorsal sac. 5. posterodorsal sac of aedeagus. 6. female subgenital plate. 7. subgenital plate variation. 8. female vagina, dorsolateral aspect, vc - vaginal cavity, rd - receptacular duct, sr - seminal receptacle, arg - accessory receptacular glands, sp - subgenital plate.



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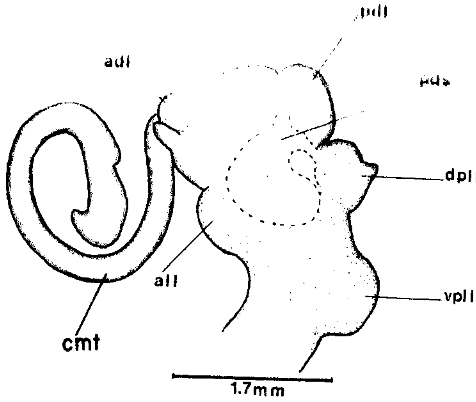

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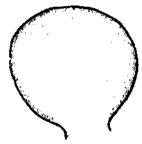

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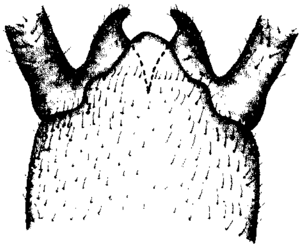

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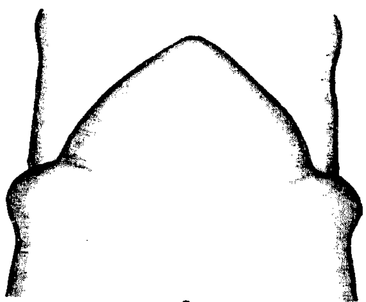

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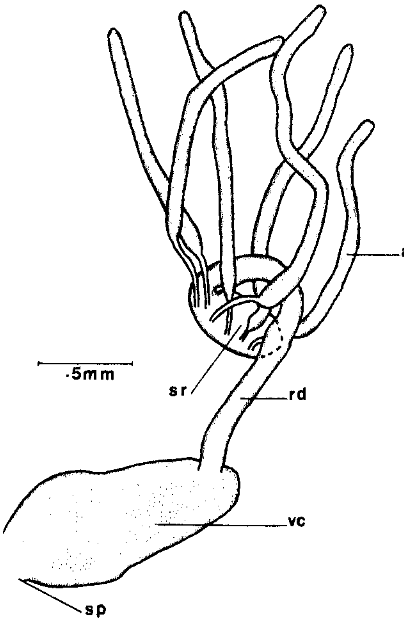

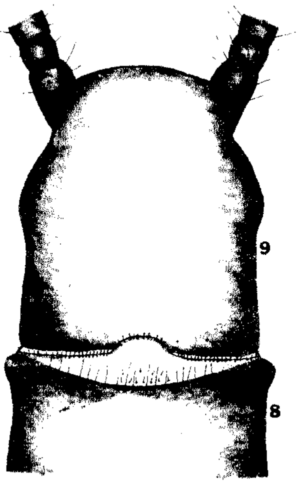

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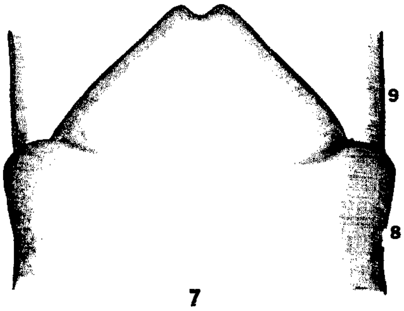

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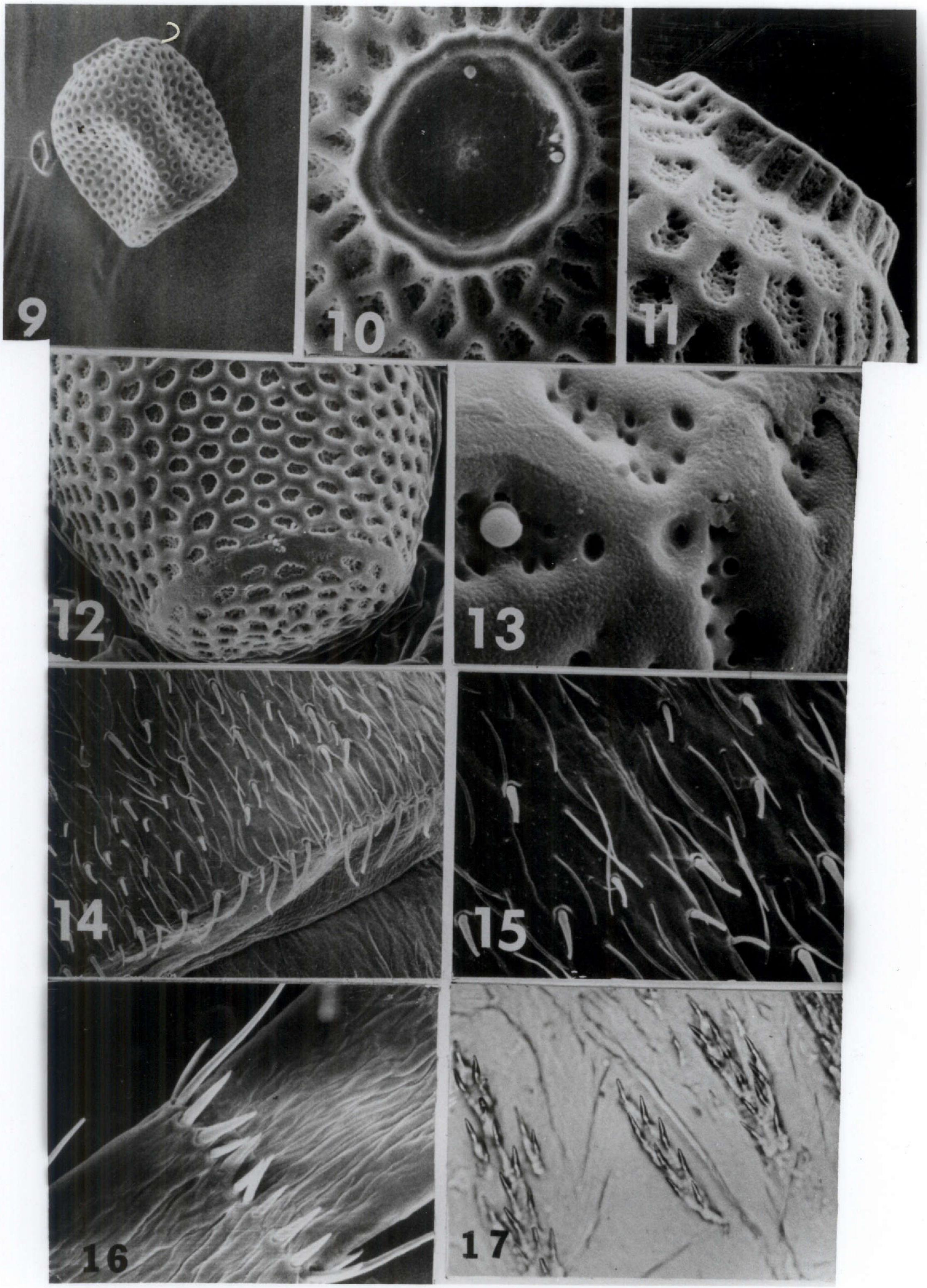
with membranous fold attached on each side near anterior margin of 9th sternum; each fold with row of short stout hairs. Apex of lobe darker than rest; and bearing row of small hairs; basal portion with few small hairs. Posterior margin of 8th sternum with row of long hairs and dark band (Fig. 3). Paraprocts produced backward into upturned hooks; apex finger-like and pointing inward; ventral surface covered with short hairs (Fig. 2). Aedeagus with 2 dorsal lobes, 1 anterolateral lobe, 2 posterolateral lobes, large dorsal sac and coiled membranous tube. Anterodorsal lobe covered with spinulae and with small membranous lobe beneath it. Long coiled membranous tube arising between antero-dorsal lobe and small membranous lobe; coiled tube with enlarged apical portion terminating in a hook (Fig. 4). Anterolateral lobe and posterolateral lobe covered with spinulae, posterodorsal lobe membranous; posterolateral lobe apically pointed. Large dorsal sac densely covered with short stout spinulae arising between posterodorsal lobe and dorsal posterolateral lobe (Fig. 4, 5). Ventral posterolateral lobe large and covered with spinulae; aedeagus encircled with spinulae up to top of ventral anterolateral lobe and to base of posterodorsal lobe.

<u>Female</u>.-- Macropterous. Body length of 11.8-14.6 mm; length of forewings 13.0-15.2 mm. Body color and external morphology similar to that of male. Subgenital plate triangular, produced from posterior margin of 8th sternum;

Plate II, Figs. 9-16. Scanning electron micrographs of *I. bilineata*.*
9. whole ova 100X. 10. detail collar top view 400X. 11. detail collar, lateral view 1000X. 12. detail of polar ring 400X. 13. detail of micropyle 3000X. 14. nymphal abdominal tergum 400X. 15. detail of nymphal abdominal tergal setal pattern 800X. 16. nymphal cercal segment 800X.

Fig. 17. Light photomicrograph of nymphal proventriculus 31.25X.

* magnifications represent original values before reduction of plate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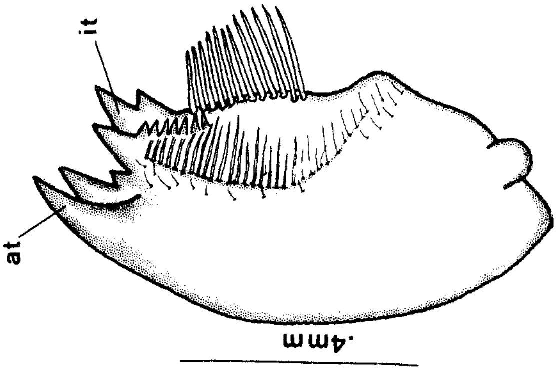
base 3/4 width of 9th sternum, apex sometimes with slight emargination (Fig. 7). Subgenital plate produced in relaxed specimens ca. 3/4 length of 9th sternum (Fig. 6, 7). Vaginal cavity lined with Y-shaped pattern of spines. Receptacular duct a long membranous tube; seminal receptacle membranous with 5-7 accessory receptacular glands lined with spinulae; tubes attaching accessory receptacular glands to seminal receptacle slender and membranous (Fig. 8).

Ova.-- Oval (specimens preserved in alcohol invaginate, giving 3-sided appearance Fig. 9); chorion covered with large regularly placed depressions, each depression with a number of small punctations (Fig. 10-12). Collar well developed (Fig. 10, 11). Apical end with polar ring (Fig. 9, 12); micropyles irregularly placed, set on ridge below polar ring (Fig. 12). Width of egg 0.39-0.42 mm; length 0.43-0.46 mm.

Mature Nymphs.-- General body color light yellow with dark markings (habitus Frison 1935, 1942). Pronotum with continuous ring of small hairs. Femur, tibia, and tarsus with fringe of long hairs. Abdomen with 3 chestnut brown longitudinal stripes, 2 lateral and one median; median stripe narrower than lateral stripes; 8 rows of longitudinal dots, 2 dorsal and 3 each laterally. Posterior margin of each abdominal segment with continuous row of stout hairs (Fig. 14); abdominal terga covered with irregularly spaced long slender and short stout hairs (Fig. 14, 15). Cerci with whorl of small stout hairs and long dorsal and ventral hair at posterior end of each segment (Fig. 16); continuous row of long dorsal hairs present after 14th segment. Proventriculus with band of 23-26 rows of short spines (Fig. 17); length of rows variable; spines pointed downward. Paraglossae produced into small knobs apically; mesal and lateral margins with row of hairs. Glossae produced slightly upward at apex; inside margins with rows of hairs. Labial palpi 3-segmented. Labium exclusive of mentum setose (Fig. 18); submentum indented ca. 1/4 the length from base. Lacinia with 2 large teeth; subapical tooth ca. 2/3 as long as apical tooth; inner lacinial margin with row of 7-10 long stout hairs; apical hair inserted between apical and subapical tooth; a row of irregular slender hairs continuing to base of lacinia below long stout hairs. Maxillary palpi with 5 segments (basal segment now shown Fig. 19); galea sword-shaped with row of fine hairs on outer margin and several short hairs at apex (Fig. 19). Mandible with 4 main teeth; apical tooth largest; 2nd tooth with small basal cusp; 3rd tooth with row of 6 small spines at base (these are best viewed at 450X); inner tooth with basal cusp ca. 1/2 of its length. Inside margin of mandible with row of 12-14 long stout hairs placed on low ridge below inner tooth; 3rd tooth with row of stout hairs starting at middle of base and continuing downward to level where stout hairs on inner margin stop; a row of

Plate III, Figs. 18-21. _I_. _bilineata_. 18. nymphal male labrum, g - glossa, pg - paraglossa, lp - labial palpus, m - mentum, sm - submentum. 19. right maxilla, nymphal male, mp - maxillary palpus, g - galea, l - lacinia. 20. right mandible, nymphal male, at - apical tooth, it - inner tooth. 21. labrum, nymphal male.



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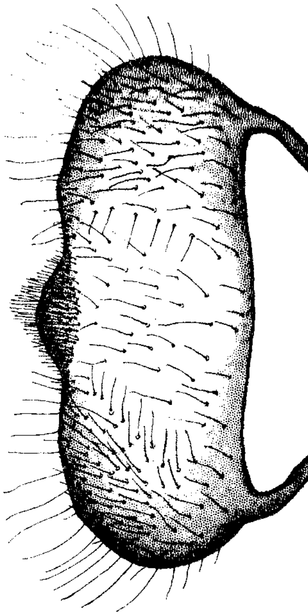

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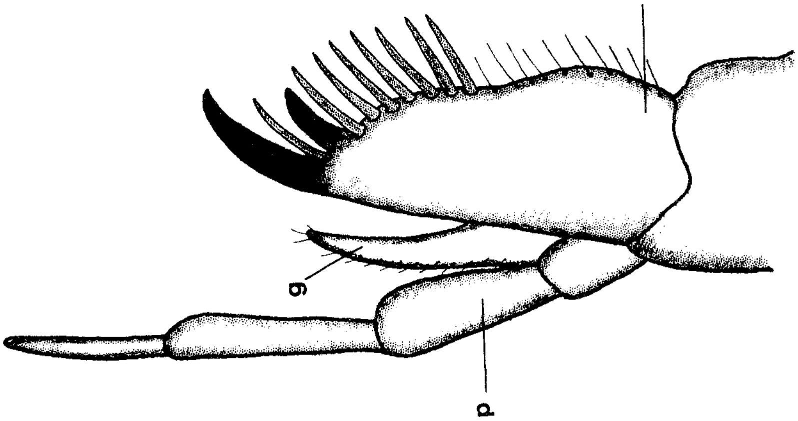

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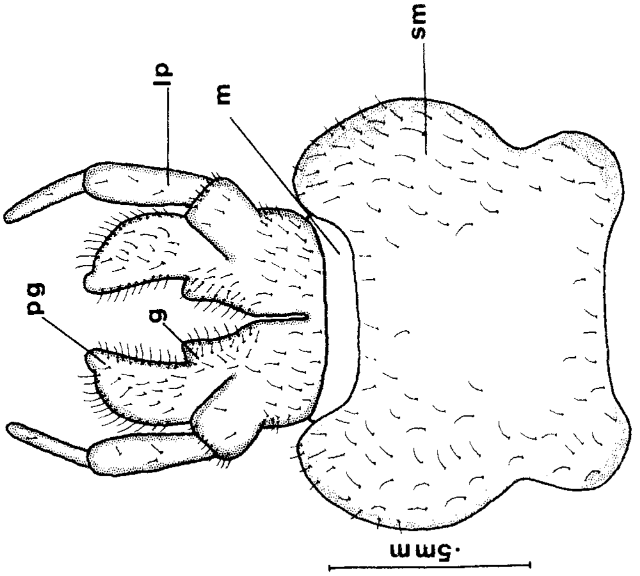

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slender hairs below stout hairs continuing outward to inner margin (Fig. 20). Labrium with median hump densely setose; entire dorsal surface covered with hairs; outer margin with longest hairs (Fig. 21).

Material.-- Neotype male, allotype, Ohio, Montgomery Co., Cincinnati, Ohio River on windows, 11/V/1951, A. R. Gaufin (SJ), deposited at USNM. CANADA: Manitoba: Winnipeg, 3/VI/1910, J. R. Wallis, 1♀ (MCZ); Ontario: Ottawa, 2/VII/1938, A. L. Melander, 1♀ (MCZ); Toronto, 1♀ (MCZ); Saskatchewan: Battleford, Junct. Hwys. N. Saskatchewan R., 29/V/1974, L. Dosdall, 3♀, 4♂ (US). United States: CONNECTICUT: Tolland Co., Storrs, 27/IV/1954, Heller, 1♀, 1♂ (SJ). ILLINOIS: Adams Co., Quincy, 17/V/1938, M. D. Farrar, 10♀, 5♂ (INHS); Quincy, 18/V/1940, C. O. Mohr and B. D. Burks, 17♂ (INHS); Champaign Co., Urbana, 30/IV/1929, A. R. Park, 1♀ (INHS); Clinton Co., Jamestown, 26/V/1928, T. H. Frison, 8♂ (INHS); Hardin Co., Elizabethtown, 22/VI/1927, T. H. Frison and R. D. C., 32♀, 22♂ (INHS); Jackson Co., Grand Tower, Miss. River, 12/V/1932, T. H. Frison, 4♀, 3♂, 6 nymphs (RWB); Jersey Co., Jerseyville, 2/V/1938, H. H. Ross and B. D. Burks, 4♀, 3♂ (INHS); Grafton, Miss. River, 20/V/1932, H. H. Ross and C. O. Mohr, 19♀, 6♂ (INHS): Kankakee Co., Kankakee, Kankakee River, 23/IV/1935, H. H. Ross and C. O. Mohr, 16 nymphs (INHS); Momence, Kankakee River, 7/V/1940, B. D. Burks, 1 nymph (INHS); Marshall Co., Henry, 3/VI/1933, C. O. Mohr, 1♀

(INHS); Mason Co., Havana, 30/IV/1914, 1♀ (INHS); Morgan Co., Meredosia, Meredosia Bay, Illinois River, 31/V/1928, D. H. Thompson, 2♀, 8♂ (INHS); Rock Island Co., Rock Island, ? 1965, Hagen 2♀ (MCZ); Rock Island, 3/VI/1930, T. H. Frison and H. H. Ross, 18♀, 17♂ (INHS); Rock Island 3/V/1931, T. H. Frison, 6♀, 12♂, 2 exuvia (INHS); Rock Island 16/V/1931, T. H. Frison and H. H. Ross, 23♀, 19♂, 11 exuvia (INHS); Rock Island, 10/V/1932, T. H. Frison, 7♀, 5 esuvia (INHS); Scott Co., Florence, 7/VI/1928, T. H. Frison, 1♀ (INHS); Whiteside Co., Prophetstown, Rock Ricker, 4/V/1932, B. D. burks, 8 nymphs (INHS); Rock Island, 27/IV/1932, T. H. Frison and C. O. Mohr, 22 nymphs (INHS). INDIANA: Knox Co., Rogers, White River, 29/IV/1936, T. H. Frison and C. O. Mohr, 3♀, 2♂, 5 exuvia (OS); Rogers, White River, 30/IV/1936, H. H. Ross and T. H. Frison, 4♂ (INHS); Petersburg, White River, 31/VI/1936, C. O. Mohr and B. D. Burks, 1♀ (INHS). KANSAS: Douglas Co., Kansas River, LeCompton Bridge, 2/IV/1976, D. Huggins, 20♀, 14♂, 27 nymphs; Riley Co., Manhattan, 3/V/1925, N. Zimmerman, 1♂ (CU); Manhattan, 10/V/1929, Marshall, 1♂ (CU). KENTUCKY: Henderson Co., Henderson, 19/IV/1938, P. O. Ritcher, 1♂ (INHS). MICHIGAN: Cheboygan Co., Douglas Lake, 29/VII/1929, C. J. D. Brown, 1♀ (RWB); Wayne Co., Detroit, ? Hubbard coll., 1♀ (MCZ). MINNESOTA: I have examined a large number of specimens from the following drainages - Blue Earth R., Elk R., Floodwood R., Kettle R., Minnesota R., Mississippi R., Rainey R., Red R., Root R., St. Croix R., and Zumbro R. (UM). NEBRASKA: Lancaster Co., Lincoln, 28/V/1923, B. D. Whelan, 1♀ (CU). NEW YORK: Thompkins Co., Ithaca, 26/V/1926, ?, 1♀ (INHS). OHIO: Athens Co., Athens, 3/V/1938, W. Stehr, 1♂ (RWB); Butler Co., New Miami, 7 Mile Creek, 28/V/1953, 1♂ (RWB); Franklin Co., Columbus, 5/VI/1961, G. Kelly, 1♂ (UK); Hamilton Co., Cincinnati, at window lights, 3/VI/1951, A. R. Gaufin, 1♀, 2♂ (UU); Hocking Co., Hocking Forest, Hwy. 664, 21/V/1953, A. R. Gaufin, 25 nymphs (UU); Licking Co., 8/V/1932, M. Neiswender, 1♀ (OSU); Montgomery Co., Dayton, Northridge, 2122 10th St. at porch light, Great Miami River, 2/VI/1951, A. R. Gaufin, 7♂ (RWB). WISCONSIN: Columbia Co., Wisconsin Dells, Wisconsin R., 5/VI/1936; T. H. Frison and H. H. Ross, 8♀ (INHS); Dunn Co., Chippewa R., 20/V/1969, W. L. Hilsenhoff, 2 nymphs (UW); Pepin Co., Curand, 15/VI/1930, W. L. Hilsenhoff, 5♀, 5♂ (UW); Rock Co., Lake Koshkanong, near Edgerton, 9/VII/1947, H. S. Dybus, 1♀, 4♂ (SJ).

Literature Records.-- Canada: New Brunswick, Newfoundland. United States: Colorado, New Jersey, North Carolina, Pennsylvania.

Diagnosis.-- As indicated by Frison (1935), *I. bilineata* is most closely related to *I. richardsoni* Frison. The nymphs are easily separated on the basis of mouthpart characters and color pattern. The differences in the laciniae are most pronounced. In *I. richardsoni*, the long stout hairs below the subapical tooth are bunched closely together and set on an elevated ridge, and the lacinia is enlarged at the base. In _I_. _bilineata_, the lacinal hairs continue 1/2 the length of the lacinia and are set on a low ridge (Fig. 19). The glossae of _I_. _richardsoni_ are distinctly pointed upward, but in _bilineata_, they are more rounded and only slightly produced upward (Fig. 18). No differences were found in the mandibles of the 2 species. The lower angles of the pronotum in _I_. _richardsoni_ have an irregular row of long hairs; in _I_. _bilineata_ there is a continuous row of small stout hairs around the pronotum.

The males are difficult to separate on the basis of external morphology, but they can be separated by aedeagal characters since _I_. _richardsoni_ does not have a large dorsal sac covered with spinulae or a long coiled membranous tube.

The females differ in the shape of the subgenital plate. In _I_. _bilineata_, the subgenital plate is produced posteriorly into a triangle which covers ca. 3/4 the length of the 9th sternum (Fig. 6, 7). In _I_. _richardsoni_, it is evenly rounded at the posterior margin and produced backward not more than 1/4 the length of the 9th sternum.

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Fig. 1. Frontisepiece-*Cascadoperla trictura* ova.

PART II

CHAPTER I

INTRODUCTION

The stonefly genus *Isoperla* was first established in 1906 when Banks split *Chloroperla* into *Isoperla*, *Alloperla* and *Chloroperla*. *Isoperla bilineata* (Say) was assigned as the genotype, and it was originally placed in the family Perlidae (Banks, 1906b, 1907a), although no type specimens were designated until 1978 (Szczytko and Stewart 1978). This classification scheme was accepted by early plecopterists, until 1940 (Needham and Claassen 1925, Claassen 1931, 1940).

Frison (1935) moved the *Isoperla*, as the subfamily Isoperlinae, into the Chloroperlidae, due to their lack of gills or gill remnants in nymphs and adults; presence of gills in nymphs is characteristic of all Perlidae. Seven years later, he proposed the group be given family status as the Isoperlidae since it was distinct from, but had characters in common with, both Perlidae and Perlodidae (Frison 1942).

Banks (1947) disregarded Frison's (1935, 1942) changes, and placed the *Isoperla* in the subfamily Isoperlinae (along with Chloroperlinae, Isogeninae, Perlodinae, Calliperlinae and others) in the family Perlidae. He also split a number of Isoperla species into new genera, based upon antennae, head, femoral, wing, palpal and setal characteristics. Most important among these changes were: (1) Perliphanes phaleratus (Needham) was placed in the Perlodinae, (2) Occiperla pinta (Frison), Calliperla luctuosa (Banks) and others went into the Calliperlinae, (3) Clioperla clio (Newman), Megahelus bellonia (Banks) and others were assigned to the Isogeninae, and (4) Nanoperla minuta (Banks) = Isoperla nana (Walsh), Washioperla signata (Banks), Perliola quinque-punctata (Banks) and all other Isoperla species into the Isoperlinae. Illies (1966), based on personal recommendation by W. E. Ricker in 1963, recombined all of these genera except Calliperla into Isoperla.

Ricker (1943, 1952), proposed that the Isoperlinae should be shifted from the Perlidae to Perlodidae, since the nymphs are separated from all other Perlidae by absence of thoracic gills and pointed paraglossae, and from the Chloroperlidae by the flatter nymphal body and 2-branched A_2 forewing veins that leave the anal cell separately. Recent workers have accepted this classification (Harden and Mickel 1952, Jewett 1959, 1960, Gaufin et al. 1966, 1972, Illies 1966, Zwick 1973, Hitchcock 1974, Szczytko and Stewart 1977, 1978, Baumann et al. 1977 and Surdick and Kim 1976). Ricker (1952) suggested that the Isoperlinae developed from an Isogenus ancestor, by reduction and loss of the supra-anal process, by movement of the ventral lobe from the 7th to the 8th sternum, and by modification of the paraprocts into hooks. He also indicated that the subfamily Isogeninae is most primitive, and the Perlodinae and Isoperlinae more specialized. The Isoperlinae shares absence of thoracic gills with the Perlodinae, and loss or reduction of the male epiproct with the Perlidae (Ricker 1952).

Illies (1966) included the genera Calliperla Banks, Isoperla Banks, Mesoperlina Klapalek and Rickera Jewett in the Isoperlinae (Perlodidae). Zwick (1973) added Bulgaroperla Rauser and Kaszabia Rauser to the subfamily.

As now classified, then, the Isoperlinae includes 3 Nearctic genera Rickera, Isoperla and Calliperla. I will propose a 4th North American genus Cascadoperla in this paper, to which is now assigned the single, distinct species trictura (Hoppe) (previously Isoperla trictura). The world and Nearctic Isoperla now number 125 and 57 species, respectively, and 21 are currently recognized from western North America. The other 68 species are from the Palearctic, making the genus exclusively holarctic.

Difficulties in classification in the group has, in part, been due to the morphological homogeneity among the Isoperla and the fact that no sustained comparative study has been made of the genus. This problem has been recognized for a long time, and active world Plecopterists brought it forward as a high priority subject needing study, during the V and VI International Plecoptera Symposia in Washington, D. C., Sept., 1975 and Schlitz, West Germany, Aug., 1977. Because of this need and the exciting challenge offered by this interesting group of stoneflies, I have undertaken the difficult task of revision and study of the drumming behavior and biology of the Nearctic species. Several Plecopterists have given me encouragement, including S. G. Jewett who initiated serious study of the genus in the 1960's. Earlier, unpublished studies of _Isoperla_ were made by J. F. Hanson in the 1940's. At present, separation of adults is often difficult, and in most cases nymphs have remained uncorrelated, and therefore undescribed or poorly described.

My approach to this problem, of necessity, is one in at least two stages, due to size of _Isoperla_. This work represents the first of those stages, the study of the 21 western North American species. My work over the past 5 years suggests that the eastern and western species probably have different origins in North America. Western nymphs have less distinct mouthparts and color patterns, and gravid females containing mature eggs are common in collections. The latter is not the case with eastern females, due apparently to some behavioral peculiarity of the life cycle, such as maturing of eggs while in the streamside forest canopy. I have maintained that the revision should include, as much as possible, comparative morphological characterization of all life stages and both adult sexes, according to arguments for holomorphological study in phylogeny by Henning (1966) and Ross (1974). This has necessitated rearing as many nymphs as possible, and a detailed SEM study of eggs of all species. Previous adult descriptions have not generally included analysis of the distinctive external and internal genitalia, and eggs of *Isoperla* have only been characterized as to shape, color and size for a few species (Knight, Nebeker, Gaufin 1965 a, b). This research is intended to serve as a foundation and model for eventual revision of the entire genus and subfamily.

CHAPTER II

MATERIALS AND METHODS

In addition to extensive field studies, collection and rearing, over 5,000 Isoperla specimens from all known University, museum and individual sources were examined. Cooperating individuals and their University affiliations that loaned specimens were: Dr. R. W. Baumann, and Dr. S. L. Wood, Brigham Young Univ. (BYU); Dr. D. B. Donald, Canadian Wildlife Service-Univ. of Calgary (UC); Dr. S. D. Smith, and Mr. D. Dunster, Central Washington State Univ. (CWS); Dr. J. V. Ward and Mr. L. J. Grey, Colorado State Univ. (CSU); Mrs. J. A. Schafrik, Cornell Univ. (CU); Dr. R. L. Newell, Idaho State Univ. (ISU); Dr. C. H. Triplehorn, Ohio State Univ. (OSU^1); Dr. N. H. Anderson, Oregon State Univ. (OSU^2); Dr. J. Linam, Southern Colorado State Univ. (SCS); Dr. P. H. Freytag, Univ. of Kentucky (UK); Dr. J. F. Hanson, Univ. of Massachusetts (UM^1); Dr. A. R. Sheldon, Univ. of Montana (UM^2); Dr. P. P. Harper, Univ. of Montreal (UM^3); Mr. L. Dosdall, Univ. of Saskatchewan (S); Dr. A. R. Gaufin, and Mrs. R. Surdick-Pifer, Univ. of Utah (UU); Dr. G. F. Knowlton, Utah State Univ. (USU); Dr. W. Turner, Univ. of Washington (UW); and Mr. S. T. Elliott, Alaska Dept. of Fish and Game (AFG).

Curators and directors of major institutional museums that loaned specimens were: Dr. D. C. Rentz, California Academy of Sciences Museum (CAS); Dr. J. E. H. Martin, Canadian National Museum (CNM); Dr. D. W. Webb and Dr. J. Unzicker, Illinois Natural History Survey Museum (INHS); Dr. C. L. Hogue, Los Angeles County Museum of Natural History (LCMNH); Dr. P. Zwick, Max Planck Institute for Limnology (MPIL); Ms. M. K. Thayer, Comparative Zoology at Harvard Univ. (MCZ); Dr. O. S. Flint, Jr., Museum of Natural History, Smithsonian (USNM); and Dr. S. Rohwer, Thomas Burker Memorial Washington State Museum (TBM).

In addition, the following individuals loaned specimens from their extensive personal collections: Dr. B. P. Stark (BS), Mississippi College, Dr. R. W. Baumann (RB), Brigham Young Univ., Dr. W. E. Ricker (WR), Fisheries Research Board of Canada, Jr. L. J. Grey (LG), Colorado State Univ., Mr. S. G. Jewett (SJ), Westt Linn, Oregon, Mrs. R. Surdick-Pifer (RP), Univ. of Utah, Dr. J. A. Stanford (JS), North Texas State Univ., and Dr. D. G. Denning (DD), Moraga, California. Abbreviations for collections of the author is Stanley W. Szczytko (SWS) and North Texas State Univ. (NTSU).

Field collecting trips were made to Colorado and New Mexico in Oct., Dec., 1974, and Jul., 1975. Two extensive trips, timed to coincide with full seasonal development of nymphs and/or emergence, were made in May, 1976, and May-Jun., 1977, to Colorado, New Mexico, Oregon, Utah, Washington, and Wyoming. Travel was supported by National Science Foundation Doctoral Dissertation Improvement Grant #DEB 76-15454 and the Faculty Research Fund of North Texas State University. Nymphs were collected live from selected and new localities for rearing and correlation with adults. Successfully reared virgin adults were also utilized in a concurrent study of *Isoperla* drumming behavior.

Nymphs were maintained in 6-pac styrofoam containers, sometimes kept on ice in larger ice chests while in the field. Containers were checked daily, and correlated adults, exuviae, and nymphs were preserved in 70 percent ETOH or adults were temporarily utilized in drumming experiments.

The aedeagii of live males were everted just prior to fixing, by gently squeezing and rolling the abdomen between the thumb and forefinger, toward the posterior end. This provided better material for study, and saved the great amount of time and laborious procedure of extruding aedeagii of preserved specimens. This procedure is highly recommended to stonefly collectors, since spines and other sclerotized parts in some taxa often prevent successful, full eversion of the aedeagus in preserved specimens.

The aedeagii of preserved specimens were everted for study by the following method: (1) specimens were removed from alcohol preservative, placed in distilled H_2O and allowed to hydrate for approximately 5 min. (this step prevented the abdomen from rupturing when the KOH was heated), (2) it was then placed in a small beaker with 10 percent KOH and heated slowly over a hotplate until the specimen began to swirl, prior to boiling, (3) the specimen was allowed to rehydrate in distilled H_2O for 1 min. (the abdomen would often rupture from increased pressure if this time frame was not strictly followed), (4) the aedeagus was everted by placing a small bent "L-shaped" probe, made from a #1 insect pin behind the 9th sternum, directly below the cerci and paraprocts, then gently exerting a slight pressure by pushing another "L-shaped" probe posteriorly down the abdomen (extreme care must be taken at this point not to create too much internal pressure, which ruptures the aedeagal sac). In some cases this basic process was aided by teasing the unextruded lobes or spines until the hydrostatic pressure caused continued eversion, (5) after successful eversions, the abdomen was clipped from the body for ease of positioning and examination. Shape and lobation of the aedeagus, its patterns of spinulae, and sclerotized structures were studied critically at 187.5X using a Wild M5 Steromicroscope on Dark Field Base, fitted with a 2X objective converter, and drawn using a Wild Drawing Attachment.

Steps 1-3 above were followed in preparing females for study of internal genitalia. The vaginal cavity, spermatheca, receptacular duct and accessory glands were then carefully dissected out for study and illustration.

Mature ova from preserved gravid females were prepared for SEM study by the following method: 1. they were sonicated in a small BEEM[R] capsule containing 90 percent ETOH for 1.5 min., using an E/MC RAI ultrasonic cleaner, 2. sonicated ova were kept in 100 percent ETOH for approximately 20 min., transferred to 90 percent amyl acetate for 15 min., then kept in 100 percent amyl acetate for 10-12 min., 3. they were then individually air dried on the tips of light-touch forceps, and then attached to an aluminum specimen stub, using Scotch brand double stick tape No. 292-030, 4. stubs were coated with ca. 200 Å of gold, using a Film-Vac Mini-Coater EMS-41 for 2 min. at a voltage of 10 milliamps.

Prepared ova were studied using an International Scientific Instruments Mini-SEM 151 scanning electron microscope. Views of micropyles, chorionic sculpturing and reticulations, attachment structures, collar areas, and whole ova were photographed at several magnifications. Occasionally, when circumstances and time allowed, ova from live females were placed in a depression cell with distilled H_2O, and studied with a Zeiss Model 4721816 light microscope. This was helpful in interpreting any size and shape changes due to preservation, and nature and proliferation of the gelatinous matrix when first placed in H_2O (simulated oviposition).

Nymphs whose mouthparts and proventriculi were to be studied, were prepared according to the aedegii study steps 1-3 outlined above. These parts were then dissected out, using minuten pin probes and scalpels, placed in 80 percent ETOH, then transferred directly to a slide mount using Hoyer's Mounting Medium #37W9700. The paraglossae, glossae, mentum, submentum, maxillae, mandibles, and labrum were drawn with the Wild M-5 and camera lucida. Size, shape, and number of rows of proventricular teeth were photographed with the Zeiss Photomicrography setup. Nymphal head-pronotum pigment patterns and tergal setation were drawn.

CHAPTER III

RESULTS

Systematic List of Western Nearctic *Isoperla* Species Complexes and the Monotypic *Cascadoperla*, According to Holomorphological Relationships

Genus *Isoperla*

I. quinquepunctata complex:	*I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, *I. quinquepunctata* (Banks)
Unassigned species	*I. katmaiensis* (new species)
I. phalerata complex:	*I. phalerata* (Needham), *I. pinta* Frison
I. sobria complex:	*I. sobria* (Hagen), *I. gravitans* (Needham and Claassen), *I. tilasqua* (new species)
I. marmorata complex:	*I. fulva* Claassen, *I. marmorata* (Needham and Claassen)
I. sordida complex:	*I. acula* Jewett, *I. adunca* Jewett, *I. bifurcata* (new species), *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and

Christenson, _I. rainiera_ Jewett, _I. sordida_ Banks

Genus _Cascadoperla_ (new genus)

C. trictura complex: _C. trictura_ (Hoppe)

Keys to the western Nearctic _Cascadoperla_ and _Isoperla_

Adult Males

1. Tenth tergum partially cleft, genital hooks developed from posterior margin of 10th tergum, paraprocts blade-like, weakly sclerotized, rounded at tips, not attached to base of cerci (Pl. XXVIII, Figs. 3 & 7). . . . . ._Cascadoperla trictura_ p. 258

Tenth tergum entire, genital hooks developed as sclerotized, modified paraprocts pointed or blunt at tips, and attached to base of cerci. . . . . _Isoperla_ (2) p. 51

2. (1). Pronotum checkered black on yellow, paraprocts with blunt tips and acute ventral spine (Fig.) . . . .(3)

Pronotum not checkered black on yellow, paraprocts variable, usually without ventral spine . . .(4)

3. (2). Ninth tergum with bipartite mesal patch of stout spinulae (Pl. VII, Fig. 4), apex of aedeagus without scattered long hair-like spinulae (Pl. VII, Fig. 7). . . . . ._I. phalerata_ p. 109

Ninth tergum with entire mesal band of stout spinulae (Pl. IX, Fig. 4), apex of aedeagus with scattered long hair-like spinulae (Pl. IX, Fig. 7). . . . . _I_. _pinta_ p. 121

4. (2). Aedeagus completely membranous. . . . . . .(5)
Aedeagus bearing a variable sclerotized process . . . . (12)

5. (4). Ninth and/or 10th terga bearing bipartite patches of long stout setae or short spinulae . . .(6)
Ninth and 10th terga devoid of long stout setae or spinulae. . . . .(10)

6. (5). Ninth and 10th terga bearing bipartite mesoposterior patches of long stout setae (Pl. IV, Fig. 2), aedeagus with 2 large mesolateral lobes bearing small fine spinulae. . . _I_. _quinquepunctata_ p. 82
Ninth tergum bearing bipartite mesoposterior patch of long stout setae or spinulae, 10th tergum void of spinulae, or stout setae, aedeagus without 2 large mesolateral lobes. . . . . (7)

7. (6). Vesicle truncate (Pl. III, Fig. 2), paraprocts short and stout (Pl. III, Figs. 4 & 5), apex of aedeagus tube-like bearing fine spinulae (Pl. III, Fig. 8). . . . . _I_. _mormona_ p. 72
Vesicle not truncate, paraprocts elongate and tapered, apex of aedeagus not tube-like. . (8)

8. (7). Wings macropterous, apex of aedeagus with 2 antero-dorsal, and 2 posterodorsal rounded lobes and 2

short posterior tubular processes (Pl. I, Fig. 5). . . . . *I. longiseta* p. 62

Wings brachypterous, apex of aedeagus without paired dorsal lobes and tubular processes elongate. . . . . (9)

9. (8). Interocellar area of head dark (Pl V, Fig. 1), vesicle petiolate (Pl. V, Fig. 2), aedeagus with 2 long dorsal tubular processes (Pl. VI, Fig. 4). . . . . . *I. katmaiensis* (new species) p. 98

Interocellar area of head light, vesicle broadly rounded posteriorly, wide at base, aedeagus with a single long dorsal tubular process. . . . . *I. jewetti* p. 60

10. (5). Vesicle obsolescent, paraprocts tapering to long fine tips, (Pl. X, Figs. 7 & 8), aedeagus with one band of long hair-like spinulae (Pl. X, Fig. 2), apex bearing 2 pointed lobes (Pl. X, Fig. 2). . . . . *I. sobria* p.133

Vesicle developed, paraprocts short, aedeagus with 2 or no bands of hair-like spinulae, apex not bearing 2 pointed lobes. . . . . (11)

11. (10). Pronotum with 2 wide, dark concolorous, longitudinal bands bordering median light stripe, rugosities absent (Pl. XII, Fig. i), vesicle lighter than rest of 8th sternum (Pl. XII, Fig. 2), aedeagus without long hair-like spinulae (Pl. XII, Figs. 5 & 6). . . . . *I. gravitans* p.144

Pronotum light brown with dark brown rugosities and median light stripe (Pl. XIII, Fig. 1), vesicle darker than rest of 8th sternum (Pl. XIII, Fig. 2), aedeagus with 2 posterior patches of long hair-like spinulae (Pl. XIII, Fig. 5). . . . .*I. tilasqua* p. 149

12. (4). Vesicle wide at base and broadly rounded, dorsal arms of sclerotized aedeagal process not forked, club-shaped bearing various small spines at apex. . . . .(13)

Vesicle variable and stalked, dorsal arms of sclerotized aedeagal process forked, not club-shaped. . . . .(12)

13. (12). Paraprocts long and tapered, recurving over 10th tergum (Pl. XIV, Fig. 4), apex of aedeagus enlarged bearing large rounded spinulae (Pl. XIV, Fig. 5), sclerotized process flattened laterally, blade-like (Pl. XIV, Fig. 5). . . . *I. marmorata* p. 158

Paraprocts short, stout not recurving over 10th tergum (Pl. XVI, Figs. 6 & 8), apex of aedeagus with 2 large conical lobes mostly spinule free (Pl. XVI, Figs. 6 & 8), sclerotized process not flattened laterally, tip ladle-like (Pl. XVI, Fig. 4). . . . .*I. fulva* p. 166

14. (12). Interocellar area of head mostly dark, never entirely light. . . . .(15)

Interocellar area of head entirely light..(18)

15. (14). Paraprocts thin, long, narrow, tapering to long fine point (Pl. XXVII, Fig. 4), sclerotized aedeagal process forked, arms short and rounded, tips bearing row of small stout spines (Pl. XXVII, Figs. 3 & 6). . . . . . .I. sordida p. 244

Paraprocts variable, not elongate and finely tapered, dorsal arm of sclerotized aedeagal process unforked and variable. . . . . . .(16)

16. (15). Vesicle narrow at base and lateral margins parallel (Pl. XXII, Fig. 2), head pattern light between ocellar triangle and base of antennae (Pl. XXII, Fig. 1), sclerotized process of the aedeagus small, short, rod-like, slightly expanded at tip (Pl. XXII, Fig. 4). . . . . .I. adunca p. 197

Vesicle petiolate, medium brown pigment band connecting base of antennae to ocellar triangle, sclerotized process of aedeagus variable, not rod-like. . . . . (17)

17. (16). Paraprocts stout, deflected downward at apex to sharp points, (Pl. XXV, Fig. 2), dorsal arm of sclerotized aedeagal process developed into single long, curved, tapered, needle-like process. . . . . .I. petersoni p. 266

Paraprocts wide at base, tapering to short fine tips, not deflected downward at tips (Pl. XXVI, Figs. 6 & 7), dorsal arm of sclerotized aedeagal process short, stout, apex expanded with 2 sharp lateral downward deflecting spines (Pl. XXVI, Figs. 5 & 9). . . . . . *I. rainiera* p. 238

18. (14). Mesoposterior margin of 9th tergum bearing patch of stout barrel-like spinulae and long fine hairs (Pl. XVIII, Fig. 4), vesicle rectangular (Pl. XVIII, Fig. 2). . . . . . . *I. acula* p. 193

Mesoposterior margin of 9th tergum devoid of spinulae and long hairs, vesicle variable, not rectangular. . . . . (19)

19. (18). Dorsal arms of forked sclerotized aedeagal process short and rounded (Pl. XXII, Figs. 3 & 5), vesicle with lateral margins parallel, rounded posteriorly (Pl. XXII, Fig. 6). . . . . *I. denningi* p. 210

Dorsal arms of forked sclerotized aedeagal process long and pointed at tips, vesicle variable, lateral margins not parallel. . (20)

20. (19). Vesicle truncate (Pl. XXI, Fig. 3), dorsal arms of sclerotized aedeagal process not extending beyond length of base, tips with ventral spine (Pl. XXI, Figs. 4 & 7). . . *I. bifurcata* p. 201

Vesicle not truncate, expanding apically and evenly rounded posteriorly (Pl. XXIII, Fig. 3), dorsal arms of sclerotized aedeagal process extending well beyond length of base (Pl. XXIII, Figs. 5 & 7), curled blunt ventral spine near fork, crossed near tips. . . . . I. fusca p. 215

Adult Females*

*Females of I. acula are unknown

1. Subgenital plate reduced to a small mesoposterior nipple (Pl. XVIII, Fig. 8), complete median dark stripe on head, darkest between ocelli, pronotum with median light stripe and 2 narrow longitudinal dark bands bordering it (Pl. XVIII, Fig. 1). . . . . Cascadoperla trictura p. 261

Subgenital plate produced and variable, head-pronotal patterns variable, without complete median stripe on head. . . . Isoperla (2) p. 51

2. (1). Pronotum checkered black on yellow, subgenital plate broadly rounded posteriorly with a median notch. . . . . (4)

3. (2). Dark band of ocellar triangle not connected between lateral ocelli, posterior margin of head completely light, (Pl. VII, Fig. 1), subgenital plate slightly angulate (Pl. VII, Fig. 6), cross veins usually present in the branches of the radial sector of forewings (Pl. VII, Fig. 5). . . . . I. phalerata p. 113

Dark band of ocellar triangle connected at lateral ocelli, posterior margin of head with median band connected to base of ocellar triangle (Pl. IX, Fig. 1), subgenital plate broadly rounded not angulate (Pl. IX, Fig. 5), cross veins absent from branches of the radial sector of forewings, (Pl. IX, Fig. 8). _I._ _pinta_ p.124

4. (2). Subgenital plate elongate, lateral margins parallel . . . . (5)

Subgenital plate variable, lateral margins not parallel. . . . .(6)

5. (4). Pronotum with 2 wide dark concolorous longitudinal bands bordering median light stripe, rugosities absent (Pl. XII, Fig. 1), subgenital plate lighter than rest of 8th sternum, light pigmentation extending to base of 8th sternum forming "V"-shaped pattern, 2 sclerotized patches on inner surface at posterolateral margins (Pl. XII, Fig. 7). . . . . . ._I._ _gravitans_ p.145

Pronotum medium brown with dark brown rugosities and median light stripe (Pl. XIII, Fig. 1), subgenital plate not lighter than rest of 8th sternum, light "V"-shaped pattern and sclerotized patches absent (Pl. XIII, Fig. 6). ._I._ _tilasqua_ p. 150

6. (4). Interocellar area mostly dark, never entirely light. . . . .(7)

Interocellar area entirely light. . . . . .(11)

7. (6). Head pattern mostly light except for dark solid ocellar triangle (Pl. XIX, Fig. 1), subgenital plate slightly triangular with deep mesoposterior notch (Pl. XIX, Fig. 5).I. adunca p. 200

Head pattern variable, not mostly light, subgenital plate variable not slightly triangular. . . . . (8)

8. (7). Pronotal rugosities distinctly rounded (Pl V, Fig. 1), subgenital plate semicircular without mesoposterior emargination (Pl. V, Fig. 6). . . . . I. katmaiensis (new species) p. 102

Pronotal rugosities irregular, not distinctly rounded, subgenital plate not semicircular.(9)

9. (8). Subgenital plate without mesoposterior emargination, posterolateral margins of 8th sternum with dark brown spots (Pl. XXVII, Fig. 8). . . . . .I. rainiera p. 241

Subgenital plate with mesoposterior emargination, posterolateral margins of 8th sternum without dark brown spots. . . . . (10)

10. (9). Subgenital plate with deep mesoposterior emargination, base distinct from posterolateral margins of 8th sternum (Pl. XXV, Fig. 6). . . . . I. petersoni p. 227

Subgenital plate with shallow mesoposterior emargination, base not distinct from postero-lateral margins of 8th sternum (Pl. XXVII, Fig. 5). . . . . *I. sordida* p. 247

11. (6). Subgenital plate semicircular or nearly so . . . .(12)

Subgenital plate not semicircular or nearly so. . . . .(14)

12. (11). Dark bands of ocellar triangle connected to base of antennae by a wide dark band (Pl. X, Fig. 1), large, dark species. . *I. sobria* p.134

Dark bands of ocellar triangle not connected to base of antennae by a wide dark band, small light species. . . . . (13)

13. (12). Pronotum evenly suffused with brown except for median light stripe, (Pl. III, Fig. 1), subgenital plate shallow, broadly rounded (Pl. III, Fig. 6). . . . . *I. mormona* p. 73

Pronotum not suffused with brown, light with dark brown rugosities and median light stripe (Pl. I, Fig. 1), subgenital plate produced, semicircular or truncate (Pl. I, Fig. 7). . . . .*I. jewetti* & *I. longiseta* pp.60,63

14. (11). Subgenital plate triangular or nearly so. . . . . (15)

Subgenital plate broadly rounded. . . . . (17)

15. (14). Subgenital plate without mesoposterior emargi-

nation usually with median nipple (Pl. XVI, Figs. 5-10), dark bands of ocellar triangle connected to base of antennae by wide dark brown "M"-shaped dark band (Pl. XVI, Fig. 1) . . . . *I. fulva* p. 171

Subgenital plate with mesoposterior emargination, dark bands of ocellar triangle not connected to base of antennae by "M"-shaped dark band..(16)

16. (15). Subgenital plate usually with a deep wide mesoposterior notch, produced 1/4 length of 9th sternum (Pl. IV, Fig. 8), abdominal segments usually with a red cast. . . . . *I. quinquepunctata* p.85

Subgenital plate with a shallow mesoposterior emargination produced 1/2 length of 9th sternum (Pl. XXII, Fig. 2), abdominal segments without a red cast . . . . *I. denningi* p. 213

17. (14). Subgenital plate slightly produced, evenly rounded (Pl. XIV, Fig. 6), anal area of hindwings fumose. . . . . *I. marmorata* p. 161

Subgenital plate produced 1/4 length of 9th sternum with slight mesoposterior emargination, anal area of hindwings not fumose . . . .*I. fusca* & *I. bifurcata* pp.218, 203

Nymphs*

*Nymphs of _I_. _acula_, _I_. _adunca_, _I_. _bifurcata_, _I_. _denningi_, _I_. _gravitans_, _I_. _katmaiensis_, _I_. _sordida_ and _I_. _tilasqua_ are unknown.

1. Occiput with transverse spinule row. . . . (2)
   Occiput without transverse spinule row. . .(9)
2. (1). Interocellar area dark. . . . .(3)
   Interocellar area light. . . . . (6)
3. (2). Laciniae with bush of long stout hairs and 3 stout spines on elevated ridge below subapical tooth (Pl. XXVII, Fig. 6), numerous long hairs irregularly placed on lateral and posterior margins of pronotum (Pl. XXVII, Fig. 2). . . . .*Cascadoperla trictura* p. 261
   Laciniae without elevated ridge, bush of long hairs and 3 stout spines below subapical tooth, few scattered long hairs irregularly placed on lateral and posterior margins of pronotum . . . . (4)
4. (3). Femora, tibiae, and tarsi without dorsal fringe of long fine hairs (Pl. XXIII, Fig. 6), meso- and meta-nota with 4 longitudinal dark brown stripes, 2 bordering median light stripe and 2 lateral (Pl. XXIII, Fig. 2). . ._I_. _fusca_ p. 219
   Femora, tibiae and tarsi with dorsal fringe of long fine hairs, meso- and meta-nota without 4 longitudinal dark brown stripes. . . . . .(5)

5. (4). Light "U"-shaped area beyond anterior ocellus, wide longitudinal medium brown bands with variable light areas bordering light median stripe of pronotum (Pl. XXV, Fig. 3). . . . . _I_. _petersoni_ p. 227

Light "U"-shaped area beyond anterior ocellus usually absent, longitudinal dark brown bands bordering light median stripe of pronotum entirely dark without light areas (Pl. XVI, Fig. 3). . . . . _I_. _fulva_ p. 171

6. (2). Pronotum wider than head, angles strongly rounded (Pl. VII, Fig. 8). . _I_. _phalerata_ p. 113

Pronotum not wider than head, angles moderately rounded. . . . . (7)

7. (6). Cerci without a continuous dorsal fringe of long fine hairs after segment 17, head pattern mostly light except for 2 quadrangular dark brown patches connecting lateral ocelli with anterior ocellus (Pl. I, Fig. 3). . . . . _I_. _jewetti_ & _I_. _longiseta_ pp.60, 63

Cerci with a continuous dorsal fringe of long fine hairs after segment 17, head pattern with medium brown patches connecting base of head to lateral ocelli and anterior ocellus with base of antennae. . . . . (8)

8. (7). Pronotum mostly light except for 2 light brown

bands near lateral margins, distinct light median stripe absent (Pl. IV, Fig. 3). . . . . *I. quinquepunctata* p.86

Pronotum medium brown with 2 wide dark longitudinal bands with variable light areas bordering light median stripe (Pl. III, Fig. 3). . . . . *I. mormona* p. 73

9. (1). Interocellar area completely dark. . . . .(10)

Interocellar area partially light . . . . (11)

10. (9). Pro-, meso- and meta-thoracic sterna with median patches of long golden brown setae (Pl. XXVI, Fig. 2), pronotal rugosities present (Pl. XXVI, Fig. 3), femora, tibiae, and tarsi without fringe of long dorsal hairs (Pl. XXVI, Fig. 10). . . . . *I. rainiera* p. 241

Pro-, meso- and meta-thoracic sterna without median patches of long golden brown setae, pronotal rugosities absent (Pl. XIV, Fig. 2), tibiae and tarsi with fringe of long dorsal hairs. . . . .*I. marmorata* p. 161

11. (9). Pronotum checkered black on yellow, upper and lower angles with a few irregularly placed long hairs (Pl. IX, Fig. 3), dark brown band on femora near distad. . . . . .*I. pinta* p.124

Pronotum with 2 wide longitudinal suffused brown bands, not checkered, upper and lower angles without a few irregularly placed long hairs (Pl. X, Fig. 3), distad of femora without dark brown band. . . . . . . I. sobria p. 134

Ova*

*Ova of I. acula are unknown

1. Collar absent . . . . (2)

   Collar present. . . . . (3)

2. (1). Cross section triangular except circular at poles, chorionic ridges elevated forming hexagonal cells, appearing reticulate (Pl. XX, Figs. 5 & 6). . . . . I. adunca p. 200

   Cross section entirely circular, chorionic ridges elevated forming deep irregular shaped depressions, not appearing reticulate (Pl. XXIV, Figs. 1-3, & 8). . . . I. bifurcata p. 203

3. (1). Chorion entirely smooth (Pl. VI, Figs. 4-6) . . . . I. katmaiensis p. 102

   Chorion sculptured not smooth. . . . . . . (4)

4. (3). Cross section a 9-sided polygon, chorion striate (Pl. VI, Figs. 1-7). Cascadoperla trictura p. 262

   Cross section circular or partially triangular not 9-sided, chorion not striate. . . . . (5)

5. (4). Chorionic ridges absent or developed slightly, not elevated. . . . . (6)

Chorionic ridges well developed, variable and elevated. . . . . (12)

6. (5). Base of collar set in a wide circular depression bordered by a low ridge, and void of chorionic sculpturing (Pl. XI, Figs. 1, 2, & 4) . . . . _I_. _sobria_ p. 137

Base of collar not set in a wide circular depression void of sculpturing. . . . . . (7)

7. (6). Cross section of anterior 1/2 triangular (Pl. II, Fig. 6). . . _I_. _quinquepunctata_ p.86

Cross section entirely circular . . . . . (8)

8. (7). Chorionic ridges evident but not elevated.(9)

Chorionic ridges not evident. . . . . . .(10)

9. (8). Collar expanded at apex (Pl. II, Figs. 1, 2, & 4), micropyles small, arranged in pairs (Pl. II, Figs. 2 & 3). . . . ._I_. _mormona_ p.76

Collar not expanded at apex (Pl. VII, Figs. 5, 6, & 8), micropyles large, arranged in threes (Pl. VII, Fig. 7). . _I_. _phalerata_ p.113

10. (8). Micropyles minute without sperm guides or grooves (Pl. XX, Fig. 2). . ._I_. _denningi_ p.213

Micropyles normal size with groove and sperm guides. . . . .(11)

11. (10). Collar well developed and elevated (Pl. II, Figs. 9 & 12). . . . . . . ._I_. _longiseta_ p.66

Collar depressed not elevated._I_. _jewetti_ p.61

12. (5). Micropyles ornate, highly elevated with one to several openings (Pl. VII, Figs. 2 & 3). . . . . <u>I</u>. <u>pinta</u> p.125

Micropyles not ornate and highly elevated, with only one opening. . . . . (13)

13. (12). Chorionic ridges narrow forming distinct hexagonal shaped cells. . . . .(14)

Chorionic ridges thickened forming variable shaped depressions. . . . .(17)

14. (13). Micropyles arranged on elevated transverse polar ridges near bottom 1/3. . . . .(15)

Micropyles not arranged on elevated transverse polar ridges near bottom 1/3. . . . .(16)

15. (14). Micropyles arranged on thickened polar ridge elevated above chorionic ridges, sperm guides absent (Pl. VIII, Fig. 10), collar distinct, crown-like (Pl. VIII, Figs. 9 & 11). . . . . <u>I</u>. <u>petersoni</u> p.230

Micropyles arranged on polar ridges not elevated above chorionic ridges, sperm guides present and elongate (Pl. XXIV, Fig. 10), collar not distinctly crown-like (Pl. XXIV, Figs. 9 & 11). . . . .<u>I</u>. <u>sordida</u> p.248

16. (14). Collar reduced (Pl. XXIV, Fig. 5), micropyles minute, arranged singularly (Pl. XXIV, Figs. 6 & 7). . . . . <u>I</u>. <u>fusca</u> p. 219

Collar well developed (Pl. XI, Figs. 9 & 12), micropyles enlarged with a small groove preceding each opening, arranged in pairs (Pl. XI, Fig. 11). . . . . . . _I_. _tilasqua_ p.150

17. (13). Collar developed slightly (Pl. XX, Fig. 8). . . . . ._I_. _rainiera_ p. 242

Collar well developed. . . . .(18)

18. (17). Chorionic ridges greatly thickened, fused and not distinct (Pl. XV, Figs. 4-6). . . . . _I_. _fulva_ p.172

Chorionic ridges distinct, not fused. . . (19)

19. (18). Collar with elevated circular ridge at base (Pl. XI, Figs. 5 & 8), chorionic depressions shallow (Pl. XI, Figs. 5-7). _I_. _gravitans_ p. 145

Collar without elevated circular ridge at base (Pl. XV, Figs. 1 & 2), chorionic depressions deep (Pl. XV, Figs. 1-3). . _I_. _marmorata_ p. 162

Isoperla Banks

Chloroperla, Pictet, 1841:276. Syn. Banks 1906.

Isoperla Banks 1906 b, 17:175. (Type species: _Isoperla bilineata_ (Say). Syn. indicated.

Suzukia Okamoto, 1912, 4:109. Syn. Ricker 1952.

Megahelus Klapalek, 1923, 63:24. Syn. Claassen 1940.

Clioperla Needham and Claassen, 1925, 2:137. Syn. Frison 1935.

Isoperla, Frison, 1935, 20:428. Syn. indicated.

Isoperla, Claassen, 1940, 232:197. Syn. indicated.

Perliphanes Banks, 1947, 54:278. Syn. Ricker i. l. 1963.

Occiperla Banks, 1947, 54:280. Syn. Ricker i. l. 1963.

Nanoperla Banks, 1947, 54:283. Syn. Ricker i. l. 1963.

Walshiola Banks, 1947, 54:283. Syn. Ricker i. l. 1963.

Perliola Banks, 1947, 54:284. Syn. Ricker i. l. 1963.

Isoperla, Ricker, 1952, 18:142. Syn. indicated.

Isoperla, Illies, 1966:392.

Isoperla, Zwick, 1973:240.

Description (western Nearctic species)

Adult-Body length: small to medium (5-18 mm). Wings: macropterous or brachypterous, clear or fumose, fork of 2nd anal vein of forewings included in anal cell so that its branches leave the cell separately. Gills: absent from thorax or abdomen. Pronotum: variable median light stripe. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Body color: variable light yellow to dark brown. Abdominal terga: usually with 3 longitudinal dark stripes, one mesal and 2 lateral.

Male terminalia-Ninth tergum: with or without patches of stout spinulae or long stout setae. Tenth tergum: entire, with or without patches of stout spinulae or long stout setae. Vesicle: variably shaped, usually developed at mesoposterior margin of 8th sternum (obsolescent in _I. ebria_). Paraprocts: sclerotized, variable, usually recurving forward to level of or over 10th tergum. Aedeagus: variable, entirely membranous or with variable sclerotized processes, bearing variable sized and shaped spinulae.

Female terminalia-Subgenital plate: developed on posterior margin of 8th sternum, variable shaped from evenly rounded to triangular. Vagina: lined with variable shaped spinulae, 6-7 long tubular accessory receptacular glands attached to seminal receptacle or receptacular duct, receptacular duct long, tubular, seminal receptacle variable shaped membranous sac.

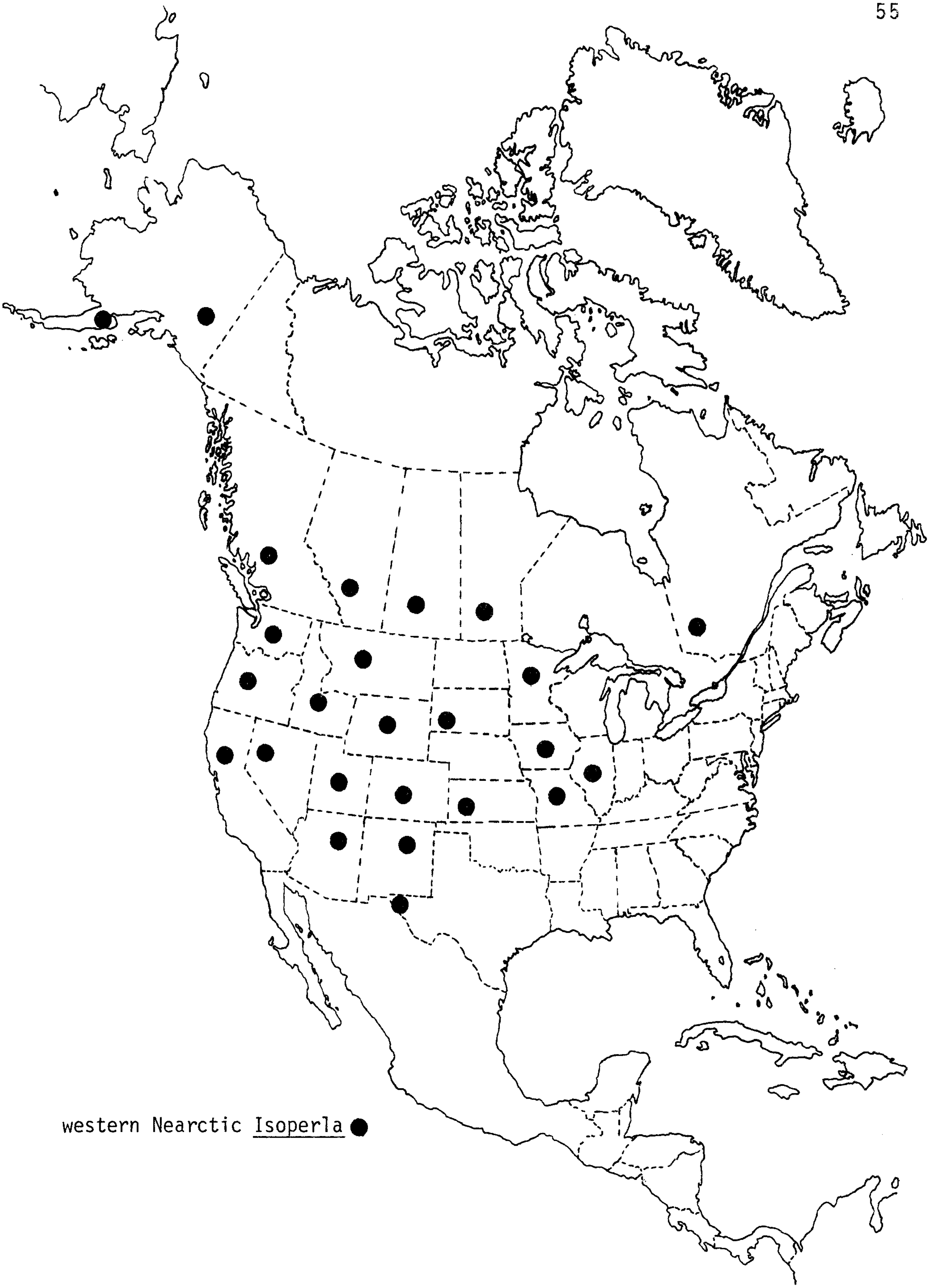
Nymphs-Body length: small to medium (7-16 mm). Body color: light yellow to dark brown. Pronotum: median light stripe (indistinct in _I. quinquepunctata_), margins fringed entirely with short stout hairs and, usually a few long hairs. Gills: absent from submentum, thorax and abdomen. Maxilla: lacinia with apical and subapical teeth, inner margin with a row of long stout hairs, maxillary palpus 5-segmented. Labrum: mesoanterior margin with nipple or small hump. Mandible: 6 teeth, inner margin with bush of long stout hairs below apical tooth. Labium: labial palpus 3-segmented, paraglossae much larger than glossae usually with small apical nipple. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Proventriculus: 23-26 variable longitudinal rows of stout, posterior projecting spinulae. Abdominal terga: usually with 3 longitudinal dark stripes, one mesal and 2 lateral.

Ova-Cross section: circular to triangular. Collar: variable, usually developed and expanded (absent in *I. adunca* and *I. bifurcata*). Chorion: usually sculptured (smooth in *I. katmaiensis*). Micropyles: variable in number arranged near bottom 1/3 on one side.

Diagnosis and Discussion

Isoperla is most similar to *Rickera* Jewett, and they share the following characters: 1. entire male 10th tergum, 2. absence of male supraanal process, 3. male paraprocts developed into genital hooks and attached to base of cerci (genital hooks not developed from 10th tergum), 4. fork of 2nd anal vein of forewings included in the anal cell so that its branches leave the cell separately, 5. lack of gills or gill remnants in nymphs and adults, 6. arms of the "Y"-shaped mesosternal ridge attached to posterior end of furcal pits in adults and nymphs, 7. wide median light stripe on adult and nymphal pronotum, and 8. three dark longitudinal stripes on nymphal abdominal terga, one narrow mesal, and 2 wide lateral. *Rickera* differs from *Isoperla* by having the male vesicle on the 7th rather than the 8th sternum, paraprocts are mostly membranous,

Fig. II. Distribution of western Nearctic *Isoperla*.



western Nearctic Isoperla ●

and the nymphal lacinia bears only one apical tooth. Males of *Isoperla* differ from the Perlodinae in that the vesicle is on the posterior margin of the 8th sternum rather than the 7th.

The genus is widely distributed throughout the western cordillera, occurring from Texas to Alaska and Illinois to California (Fig. II). The species inhabit all types of lotic systems, and emergence begins in late spring and continues throughout the summer. Most species are thought to undergo univoltine life cycles.

The name of each following western *Isoperla* species group is based on its earliest valid species representative.

Species Group A

Isoperla quinquepunctata complex

This group is composed of *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks and *I. quinquepunctata* (Banks). *I. patricia* Frison is not included here, since all morphological evidence and drumming behavior (unpublished concurrent study) indicate that it is a synonym of *I. quinquepunctata*. These species all share the following characteristics: 1. male with entirely membranous aedeagus, bearing patches or bands of small stout, or small fine spinulae, 2. 9th and/or 10th male abdominal terga with patches of long stout hairs or spinulae, 3. female subgenital plate broadly rounded posteriorly, but variable and sometimes similar to females of other groups, 4. ova with well-developed collar and relatively smooth chorion, having small punctations, and ridges reduced or absent; lower 1/3 of egg with micropyles arranged in groups of 2 or 3, only on one side, 5. faint row of occipital spinulae on nymphal head, 6. nymphal femora, tibia and tarsus with a dorsal fringe of long hairs, and 7. three longitudinal stripes on abdominal terga.

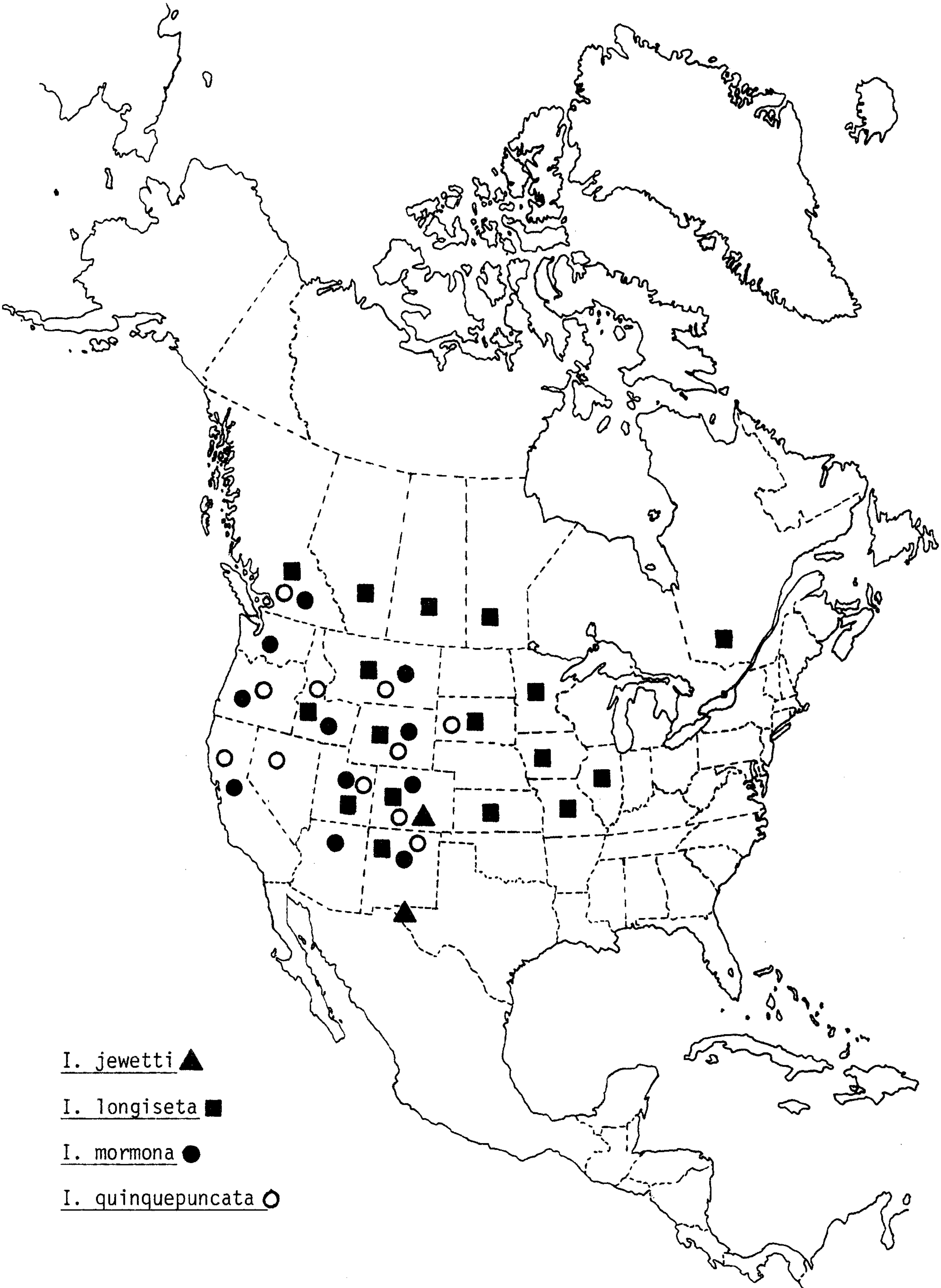
The group is widely distributed from Illinois to California and Texas to Canada (Fig. III). _I. longiseta_ and _I. jewetti_ mainly inhabit large rivers, _I. quinquepunctata_ is found in small rivers and creeks, and _I. mormona_ is found in creeks and larger rivers. The species exhibit a seasonal emergence succession with _I. quinquepunctata_ beginning in early May, especially in more southern latitudes, and _I. longiseta_ and _I. mormona_ extending until late Jun.-Aug. All species are thought to undergo univoltine life cycles.

Isoperla jewetti Szczykto and Stewart

Isoperla longiseta, Frison, 1942, 22:318. In part.

Isoperla jewetti Szczytko and Stewart, 1976, 36:215. Holotype ♂, and Allotype ♀; 5-10 mi. S. of El Paso, on rd. to Marathon, El Paso Co., Texas, USA, (INHS) (male and female genitalia, aedeagus, nymphal mouthparts, and ova).

Fig. III. Distribution of the _I_. _quinquepunctata_ complex.


I. jewetti
I. longiseta
I. mormona
I. quinquepuncata

Isoperla jewetti, Szczytko and Stewart, 1977, 103:355 (male and female genitalia, aedeagus, nymphal mouthparts, and ova).

Description

Male.-- Brachypterous. Length of forewings 1.5-2.0 mm; length of body 6-7 mm. General body color light brown. Head-pronotal pigment pattern similar to *I. longiseta* (Pl. I, Fig. 1), Ninth tergum with bipartite patch of stout setae and dark brown pigmentation. Tenth tergum with 2 dark brown patches void of setae at posterior margin (Szczytko and Stewart 1976; Fig. 10). Vesicle, broader at base than apex (Szczytko and Stewart 1976; Fig. 9). Paraprocts slender, tapering to points apically, and recurving anteriorly, slightly over 10th tergum (Szczytko and Stewart 1976; Figs. 10 & 11). Aedeagus entirely membranous with long dorsal finger-like process (Szczytko and Stewart 1976; Fig. 11).

Female.-- Macropterous. Length of forewings 8-9 mm; length of body 6-9 mm. General body color, and head-pronotal pigmentation similar to male. Subgenital plate truncate posteriorly, lateral margins parallel with sides of abdomen (Szczytko and Stewart 1976; Fig. 12).

Nymph (reared).-- Length of mature nymph 8-9 mm. Description essentially the same as for *I. longiseta* (Pl. I, Fig. 3) (see diagnosis under *I. longiseta*).

Ova.-- General shape oval, cross section circular (Szczytko and Stewart 1977; Fig. 16). Collar reduced, chorion covered with evenly spaced punctations, ridges reduced, micropyles arranged in pairs or threes near bottom 1/2, on one side.

Material examined.-- TYPES: Holotype ♂, allotype, and 6 ♂, 17 ♀, and 2 exuvia; paratypes, TEXAS, El Paso Co., 5-10 mi. S. of El Paso, on rd. to Marathon, in *Tamarix* along irrigation ditch, 22/IV/1939, J. A. and H. H. Ross (INHS). Additional specimens - COLORADO: Huerfano Co., La Veta Pass, 21/VII/1938, D. J. and J. N. Knull, 1 ♂ (INHS).

Distribution.-- USA: COLORADO and TEXAS (Fig. III).

Diagnosis and Discussion

I. jewetti is closest to *I. longiseta*, and females and nymphs cannot be separated (see discussion under *I. longiseta*).

This rare species is restricted to Texas and Colorado. Attempts to collect additional specimens from the type locality have been unsuccessful, and the population may now be extinct, due to the heavy use of pesticides in the irrigation ditches and canals in that area (Szczytko and Stewart 1976).

No life history or general biology data is available. Emergence occurs in the middle of Apr. in Texas, and the middle of Jul. in Colorado, based on the specimens examined.

Isoperla longiseta Banks

Isoperla longiseta Banks, 1906a, 38:337. Holotype ♀; Onaga Kansas, USA, (MCZ #11,336), (female genitalia).

Isoperla longiseta, Needham and Claassen, 1925, 2:156 (male and female genitalia).

Isoperla longiseta, Claassen, 1940, 232:203.

Isoperla longiseta, Frison, 1942, 21:318. In part.

Isoperla longiseta, Illies, 1966:408.

Isoperla longiseta, Zwick, 1973:247.

Additional references: *Isoperla longiseta*, Banks, 1907; Neave, 1934; Ricker, 1943 (male and female genitalia, female genitalia, female head-pronotal pattern, and forewing), 1946 & 1964; Harden and Mickel, 1952; Gaufin, 1955; Jewett, 1959; (male genitalia) Gaufin et al., 1966 (male and female genitalia), 1972 (male and female genitalia); Knight et al., 1965b (ova); Hitchcock, 1974; Stewart et al., 1974; Ricker and Scudder, 1975; Szczytko and Stewart, 1976 & 1977; Baumann et al., 1977 (male and female genitalia).

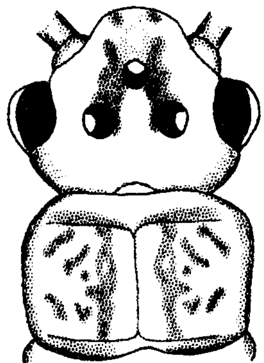
Description (Plates I and II)

Male (Pl. I).-- Macropterous. Length of forewings 6-8 mm; length of body 5-7 mm. General body color light yellow to yellowish brown. Lateral ocelli of head connected to anterior ocellus by a dark "H"-shaped pigment pattern. Interocellar space light yellow (Fig. 1). Anterior frons with 2 small pigment spots. Ninth tergum with bipartite patch of stout hair-like setae and dark brown patches void of setae at posterior margin. Vesicle broader at base than apex (Fig. 2). Posterior margin of cercal segments with very long ventral hair, medium length dorsal hair at posterior margin of segments 1-10. Paraprocts slender, tapering apically to sharp points, with small fine hairs posteriorly, and recurving anteriorly, over ca. 1/3 10th tergum (Figs. 4 & 6). Aedeagus entirely membranous bearing broad even mesal band of short stout spinulae (Fig. 5B); its posteroventral margin with band of small fine hair-like spinulae (Fig. 5A), and apex with 2 anterodorsal, 2 posterodorsal rounded lobes and 2 short posterior tubular processes (Fig. 5C-E).

Female (Pl. I).-- Macropterous. Length of forewings 8-10 mm; length of body 6-9 mm. General body color, and head-pronotal pigmentation similar to male. Subgenital plate of 8th sternum nearly semicircular, lateral margins parallel with sides of abdomen (Fig. 7).

Nymph (reared) (Pl. I).-- Length of mature nymph 8-11 mm. Dorsum of head with 2 quadrangular dark areas connecting lateral ocelli with anterior ocellus. Interocellar space light. Faint occipital ridge, with sparse, small spinulae on back of head. Pronotum fringed with short stout hairs; long stout hairs interspersed, except anterior margin (Fig. 3).

Plate I. Figs. 1-7. _I. longiseta_. 1. adult head and pronotum (scale: 1 mm = .05 mm). 2. male vesicle and 8th sternum (1 mm = .03 mm). 3. nymph head and pronotum (1 mm = .06 mm). 4. male terminalia, dorsal aspect (1 mm = .03 mm). 5. male aedeagus, lateral aspect, A. posteroventral band of small fine hair-like spinulae, B. mesal band of short stout spinulae, C. posterodorsal tubular processes, D. posterodorsal lobes, E. anterodorsal lobes (1 mm = .02 mm). 6. male paraproct, lateral aspect (1 mm = .01 mm). 7. female subgenital plate (1 mm = .03 mm).



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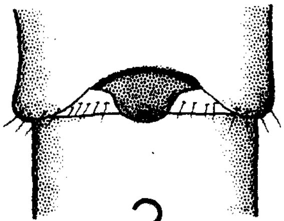

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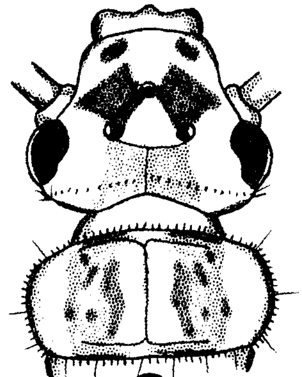

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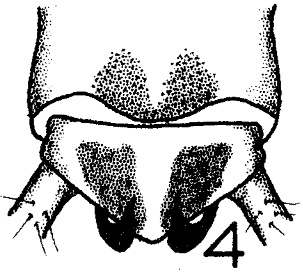

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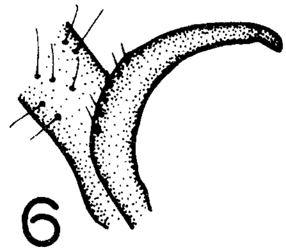

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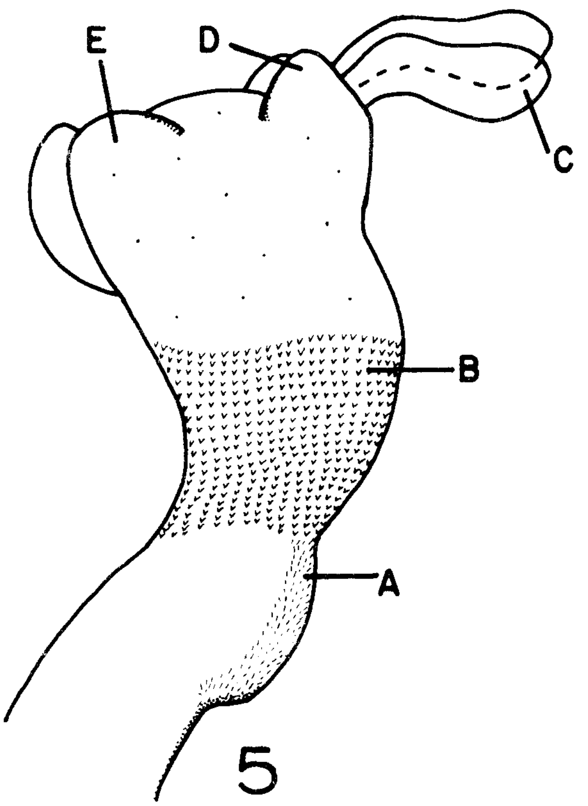

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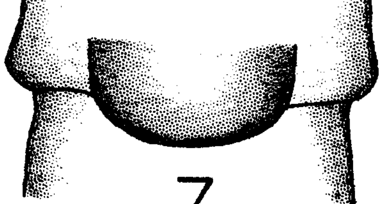


7

Abdominal terga with 3 longitudinal stripes, and 8 faint rows of longitudinal dots (sometimes absent), 2 mesal, and 3 lateral. Femora and tibiae with dorsal fringe of long fine hairs, and tarsi with shorter fringe. Posterior margin of cercal segments encircled with small stout hairs; dorsal fringe of short hairs become progressively longer segments 13-17; one long hair both ventrally and dorsally at posterior margin of remaining segments.

Ova (Pl. II).-- General shape oval, cross section circular (Fig. 9). Color honey. Length .21 mm, width .13 mm. Collar well developed, with partitioned projections; chorion covered with many evenly spaced punctations (Figs. 9-11), micropyles slightly raised, and arranged in pairs or threes near bottom 1/3, on one side (Figs. 9-11).

Material examined.-- TYPES: Holotype ♀, Kansas: Onaga, Date ?, Creveceur, (MCZ). Additional specimens: CANADA: Saskatchewan, Sutherland, 17/VI/1939, W. E. Ricker, 2♂ (WR), N. Saskatchewan, Hwy. 5, 13/VII/1973, D. Smith, 4♂, 14♀ (US). USA: COLORADO: Grand Co., 4 mi. N. of Granby, Hwy. 40, Colorado R., 24/VII/1960, Collector ?, 1♀ (UU); Moffat Co., Maybell, Yampa R., 18/VII/1968, B. R. Oblad, 3♂, 2♀ (RWB), Yampa R., 24/VI/1962, A. R. Gaufin, 1♂ (UU), Yampa R., 29/VI/1968, B. R. Oblad, 2♂ (UU). ILLINOIS: Union Co., Ana, 6/VI/1951, H. H. Ro s and Richards, 2♀ (WR). IOWA: Story Co., Ames, 10/VI/1931, P. A. Morre, 3♀ (INHS). KANSAS: Leavenworth Co., Lawrence, 26/VI/1919, Collector ?,

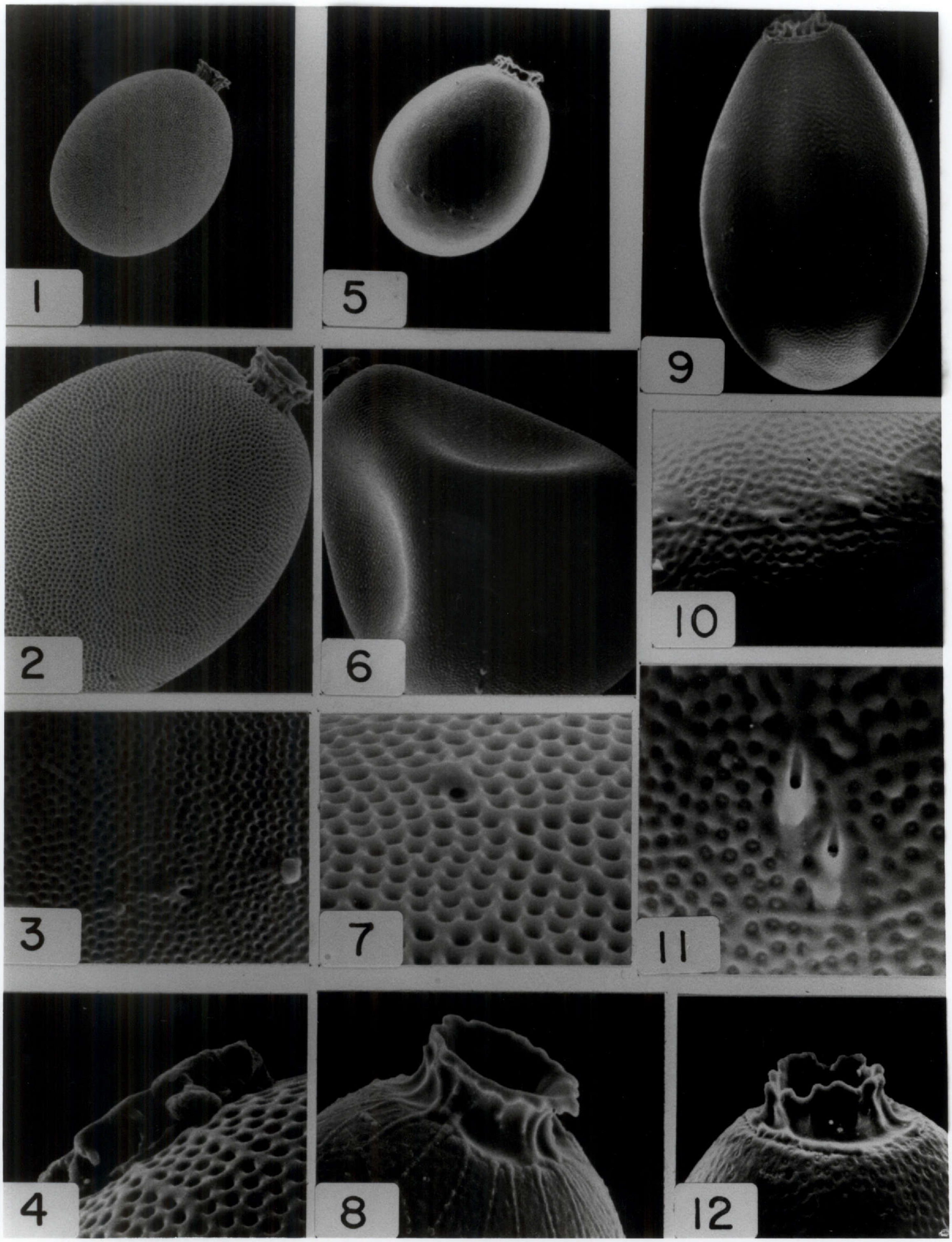
Plate II - Scanning electron micrographs of *Isoperla* ova*

Figs. 1, 2, 4 & 7. *I. mormona*. 1. whole ova 200X. 2. detail of chorion 400X. 4. detail of collar 1000X. 7. detail of micropyle 2000X.

Figs. 3, 5, 6 & 8. *I. quinquepunctata*. 3. detail of micropyle 1000X. 5. whole ova 200X. 6. detail of chorion 400X. 8. detail of collar 1000X.

Figs. 9-12. *I. longiseta*. 9. whole ova 400X. 10. detail of micropyles 1000X. 11. detail of micropyles 2000X. 12. detail of collar 1000X.

* magnifications represent original values before reduction of plates.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1♀ (CU). MISSOURI: Cole Co., Jefferson City, Missouri R., 29/V/1937, H. H. Ross, 1♂, 1♀ (INHS). MONTANA: Carbon Co., Clarks Fork of Yellowstone R., 10 mi. above Yellowstone R., 25/VI/1966, J. R. Grierson, 1♀ (UU); Custer Co., Miles City, 26/VII/1915, Collector ?, 1♂, 2♀ (CU); Dawson Co., Glendive, Yellowstone R., 14/VII/1940, H. H. and J. A. Ross, 3♂, 7♀ (INHS); Fergus Co., 70 mi. S. E. of Malta, Hwy. 191, Missouri R., 6/VII/1966, J. R. Grierson, 1♂, 1♀ (SJ); Richland Co., Sidney, Yellowstone R., 2/VII/1975, R. L. Newell, 9♂, 10♀ (ISU); Roosevelt Co., Wolf Point, Missouri R., 14/VII/1940, H. H. and J. A. Ross, 2♂, 9♀ (INHS). NEBRASKA: Lincoln Co., Lincoln, 11/VI/1944, Collector ?, 2♂ (INHS); Richardson Co., Rulo, Missouri R., 12/VI/1944, Collector ?, 1♀ (INHS). NEW MEXICO: Rio Arriba Co., San Juan R., 4/VII/1966, S. L. Jensen, 7♂, 4♀ (RWB), San Juan R., 7/VIII/1960, Coft, 3♂, 4♀ (SJ). UTAH: Carbon Co., Desolation Canyon, Green R., 8/X/1975, Winget and Reichert, 1♀ (RWB); Grant Co., Dewey, Colorado R., 15/V/1954, A. R. Gaufin, 1 nymph (UU), N.W. of Moab, Colorado R., 26/VI/1943, G. F. Knowlton, 41♂, 18♀ (INHS); Unitah Co., Bonanza, White R., 25/VII/1975, R. W. Baumann, 2♂, 1♀ (RWB), below Bonanza, Hwy. 45, White R., 25/V/1977, S. W. Szczytko and K. W. Stewart, 7 nymphs, reared 3♂, 1♀ (SWS & NTSU); San Juan Co., 5 mi. W. of Bluff, San Juan R., 21/VI/1966, Collector ?, 2♂ (UU). SOUTH DAKOTA: Buffalo Co., Buffalo, 19/VI/1925, H. C. Severin, 1♂, 1♀ (INHS);

Yankton Co., Yankton, Missouri R., 19/VI/1925, H. C. Severin, 2♀ (INHS). WYOMING: McKenzie Co., Yellowstone R., 4/VII/1975, R. L. Newell, 15 nymphs (ISU); Sheridan Co., Sheridan, 29/VI/1949, D. G. Denning, 1♂, 2♀ (SJ); Sublette Co., Boulder, Trib. Pine Branch R., 20/VI/1940, H. H. Ross, 1♀ (INHS); Sweetwater Co., Green R., 30/VI/1959, A. R. Gaufin, 1♂ (UU), Green R., 29/VII/1959, A. R. Gaufin, 1♂, 1♀ (UU), Green R., 12/VII/1959, A. R. Gaufin, C. Smith and Musser, 1♂ (UU), Green R., 11/VI/1959, A. R. Gaufin, 8♂, 1♀ (UU); Weston Co., Upton, 20/VI/1940, H. H. and J. A. Ross, 2♂, 1♀ (INHS).

Distribution.-- CANADA: Alberta, British Columbia, Manitoba, Quebec, Saskatchewan; USA: Colorado, Idaho, Illinois, Iowa, Kansas, Minnesota, Missouri, Montana, New Mexico, South Dakota, Utah and Wyoming (Fig. III).

Diagnosis and Discussion

I. longiseta is similar to *I. jewetti*. Males can be distinguished by their longer slender paraprocts, absence of a long single finger process dorsally on the aedeagus, and macropterous wings. I was unable to separate females and nymphs. *I. longiseta* ova are larger than *I. jewetti*, and their chorionic punctations are shallower (Szczytko and Stewart 1976, 1977).

This species extends further eastward than any other typically western *Isoperla*. Frison (1942) stated that it was associated with the prairie and plains states west of the Mississippi River, and that it was replaced in the Rocky Mountains and West Coast by *I. mormona*. Ricker (1946, 1964) indicated that it was the only typically prairie stonefly species inhabiting large river systems. No life history or biological studies have been done on this species.

Specimens available indicate that emergence begins during the first week in Jun. and continues until late Aug., with peak emergence occurring late Jun.-Jul.

Isoperla mormona Banks

Isoperla mormona Banks, 1920, 64:322. Holotype ♀; Vinyard Utah, USA, (MCZ #10,822), (female genitalia).

Isoperla marmona, Needham and Claassen, 1925, 2:153.

Isoperla insipida Hoppe, 1938, 4:157. Syn. Frison, 1942.

Isoperla marmona, Claassen, 1940, 232:203.

Isoperla mormona, Frison, 1942, 22:321.

Isoperla mormona, Illies, 1966:410.

Isoperla mormona, Zwick, 1973:247.

Additional references: *Isoperla mormona*, Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Gaufin and Jensen, 1961; Gaufin et al., 1966 (nymphal mesosternum, male and female genitalia); Ricker, 1964; Gaufin, 1964b; Knight et al., 1965b (ova); Logan and Smith, 1966; Knight and Gaufin, 1966, 1967; Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and genitalia); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (nymphal mesosternum, male and female genitalia, and habitus).

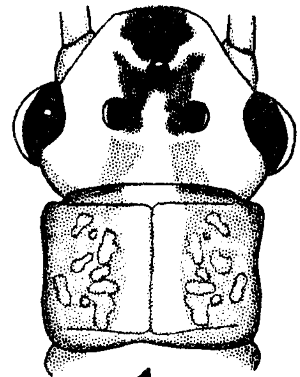
Description (Plates II and III)

Male (Pl. III).-- Macropterous. Length of forewings 7-9 mm; length of body 6-8 mm. General body color light yellow. Lateral ocelli of head connected to anterior ocellus by "H"-shaped dark brown pigmentation. Interocellar space light yellow. Anterior frons with large median dark brown pigment patch. Pronotum evenly suffused with brown except median light yellow stripe (Fig. 1). Ninth tergum with patch of short stout spinulae (Fig. 5). Posterior margin of cercal segments with long ventral hair, medium length dorsal hair at posterior margin of segments 1-10. Paraprocts short, stout, tapering apically to points and curving outward, recurving anteriorly slightly over 10th tergum (Figs. 4 & 5). Vesicle, truncate posteriorly (sometimes slightly rounded), much darker than rest of segment (Fig. 2). Aedeagus entirely membranous with an irregular large mesal patch of short, stout spinulae (Fig. 8A); anterior margin with a large rounded lobe bearing narrow anterior band of very fine spinulae (Fig. 8C); apical 1/3 tube-like, covered with fine spinulae except at bi-lobed tip (Fig. 8E), posterobasal area of apical tube with scattered patch of short, stout spinulae (Fig. 8B).

Female (Pl. III).-- Macropterous. Length of forewings 8-9 mm; length of body 6-7 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broadly rounded, produced little posteriorly (Fig. 6).

Nymph (Reared), (Pl. III).-- Length of mature nymph 6-8 mm. Dorsum of head with 2 bands of dark brown pigmentation extending from posterior margin to above occipital ridge, interrupted behind lateral ocelli then continuing to base of antennae and ending as 2 light patches encircled by pigment on anterior frons, 2 light yellow spots within dark pigment lateral to anterior ocellus, narrow light band in interocellar space. Faint occipital ridge, with sparse, small spinulae on back of head (Fig. 3). Pronotum fringed with evenly spaced small stout hairs; long stout hairs irregularly interspersed at posterior angles and margin (Fig. 3). Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal and 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Femora, tibiae, and tarsi with dorsal fringe of long fine hairs; tibia with row of short, stout spines on dorsal margin, and femur with sparse row on ventral margin. Posterior margin of cercal segments encircled by whorl of small stout hairs; medium length hairs both dorsal and ventral at posterior margin after segment 3; incomplete dorsal fringe of medium length hairs on segment 16; continual dorsal fringe of long fine hairs on 17th and remaining segments.

Plate III. Figs. 1-7. _I. mormona_. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. male vesicle and 8th sternum (1 mm = .03 mm). 3. nymph head and pronotum (1 mm = .05 mm). 4. male paraproct, lateral aspect (1 mm = .02 mm). 5. male terminalia, dorsal aspect (1 mm = .04 mm). 6. female subgenital plate (1 mm = .03 mm). 7. nymphal cerci, segs. 15-18 (1 mm = .02 mm). 8. male aedeagus, lateral aspect, A. mesal patch of short stout spinulae, B. scattered patch of short stout spinulae, C. large round anterior lobe, D. patch of small fine spinulae, E. bi-lobed apex (1 mm = .02 mm).



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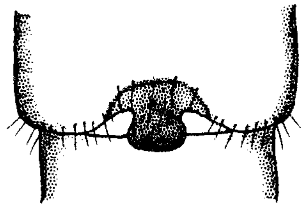

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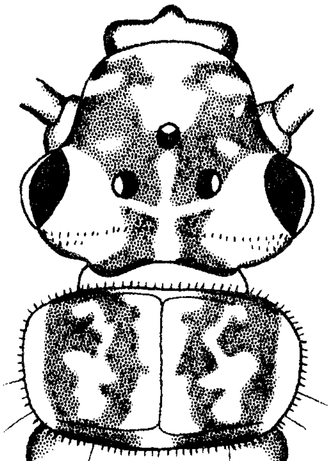

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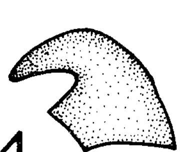

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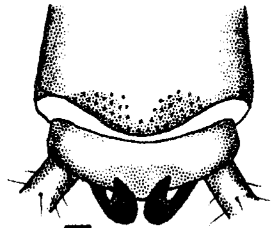

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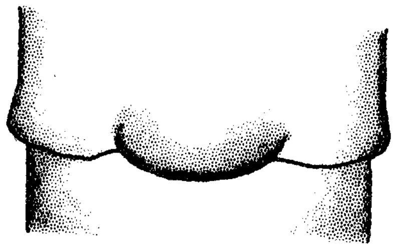

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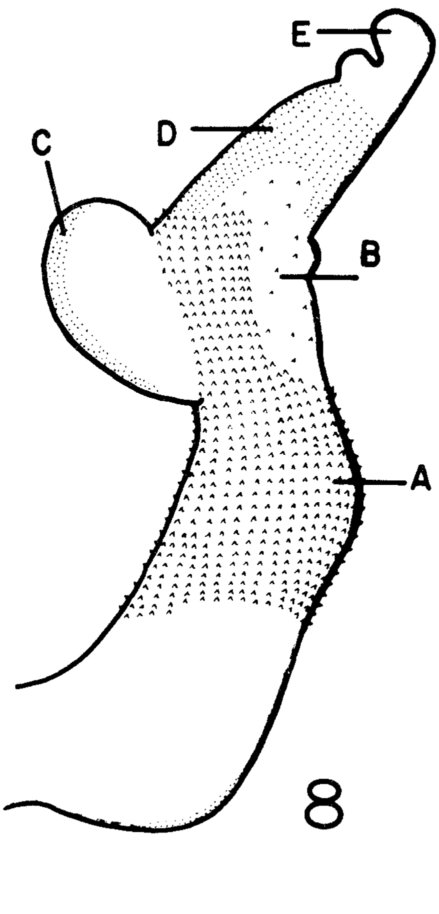

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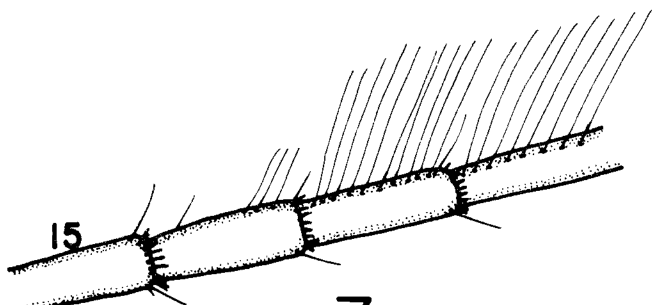

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Ova (Pl. II).-- General shape elliptical, cross section circular (Fig. 1). Color light brown. Length .25 mm, width .18 mm. Collar well developed, raised .02 mm from chorion, and expanded at apex (Figs. 1 & 2). Chorion covered with numerous evenly spaced punctations, ridges slightly raised on surface (Figs. 2 & 7). Micropyles arranged in pairs near bottom 1/3, on one side (Figs. 2 & 7).

Material examined.-- TYPES: Holotype ♀, UTAH, Vinyard, 22/VI/?, Collector ?, #10,822 (MCZ); *I. insipida* Hoppe, Paratypes, WASHINGTON, Cowlitz Co., Castle Rock, 10/VII/1932, G. N. Hoppe, 1♂, 1♀ (INHS); Kittitas Co., Cle Ellum, 3/VII/1931, G. N. Hoppe, 1♂ (INHS). Additional specimens - USA: ARIZONA: Apache Co., near Greer, Hwy. 373, Hall Crk., 19/VII/1968, R. W. Baumann, 1♀ (RWB), N. Fork White R., 27/VII/1966, R. K. Allen, 2♂, 2♀ (INHS), near Alchesay National Fish Hatchery, 17/V/1964, S. G. Jewett, 3♂, 2♀ (SJ); Coconino Co., Oak Crk. Indian Garden, 19/VI/1937, L. K. Gloyd, 3♂, 4♀ (INHS). CALIFORNIA: Los Angeles Co., Lake Elizabeth Canyon, 26/IV/1950, Collector ?, 5♂, 5♀, (LCMNH); Siskiyou Co., near Weed, unknown Crk., 10/VII/1975, D. G. Denning, 4♂, 1♀ (RWB). COLORADO: Archuleta Co., Piedra R., 7/VII/1960, A. R. Gaufin. 13♂, 15♀ (RWB), Piedra R., 23/VII/1960, L. D. Jensen, 1♂, 1♀ (RWB), 2 mi. N. of Arboles, Piedra R., 14/VII/1960, A. R. Gaufin, 50 nymphs (UU), Los Pinos R., 8/VII/1960, A. R. Gaufin, 3 nymphs (UU); La Plata Co., Ignacio, Los Pinos R., 7/VIII/1964,

A. R. Gaufin, 10♂, 12♀ (RWB); Montrose Co., 3 mi. N. of Montrose, Uncompahgre R., 15/VII/1962, Collector ?, 3♂, 6♀ (UU); Park Co., Lake George, S. Platte R., 8/VIII/1943, J. A. and H. H. Ross, 1♀ (INHS), Tarryall, Tarryall R., 15/VII/1956, H. H. Ross, 3♂, 2♀ (SJ); Rio Blanco Co., Meeker, White R., 31/VII/1960, A. R. Gaufin, 10♂, 8♀ (UU), White R., 13/VII/1961, A. R. Gaufin, 72♂, 26♀ (UU & BS). IDAHO: Ada Co., Braves Ball Park, Boise R., 15/VIII/1963, S. L. Jensen, 1 nymph (UU); Bonneville Co., Idaho Falls, Snake R., 13/VII/1948, D. R. Merkley, 1♂, 3♀ (RWB), Hwy. 26, Rainey Cr., 21/VI/1964, S. L. Jensen, 2 nymphs (UU); Fremont Co., Hwy. 32, Fall R., 8/VII/1972, R. L. Newell, 1♀ (ISU), Hwy. 191, Buffalo R., 23/VI/1964, S. L. Jensen, 8 nymphs (UU); Power Co., 10 mi. W. of Pocatello, Hwy. 30, Bannock Crk., 20/VI/1964, J. W. Richardson and S. L. Jensen, 2♂, 3♀ (UU). MONTANA: Beaverhead Co., 15 mi. S. of Dillon, Beaverhead R., 19/VI/1965, A. V. Nebeker, 3♂ (UU), 5 mi. N.E. of Dillon, Beaverhead R., 5-6/VII/1966, J. R. Grierson, 1♂, 4♀ (UU), 24 mi. N. of Dillon, Big Hole R., 5/VIII/1966, J. R. Grierson, 1♂, 1♀ (UU); Broadwater Co., Toston, Missouri R., 22/VI/1940, J. A. and H. H. Ross, 3♂, 7♀ (INHS); Cascade Co., Great Falls, Missouri R., 24/VI/1965, A. V. Nebeker, 1♂ (UU); Fergus Co., 2.2 mi. S.E. of Lewistown, Spring Crk., 5/VI/1966, J. R. Grierson, 1♂, 2♀ (UU); Glacier Co., Glacier National Park, St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 1♀ (UU); Granite Co., near Phillipsburg, Flint Crk., 6/VIII/1965, A. R. Gaufin, 10♂, 13♀ (UU); Jefferson Co., 15 mi. S.E. of Helena, Boulder R., 14/VIII/1966, J. R. Grierson, 1♂, 5♀ (UU); Madison Co., 2 mi. above Ruby Dam, Ruby R., 6/VIII/1966, J. R. Grierson, 1♀ (UU); Pondera Co., Dupuyer, Dupuyer Crk., 26/VII/1967, A. R. Gaufin, 12♂ (UU). NEW MEXICO: Catron Co., Apache National Forest, Cottonwood Campground, 13/VII/1967, R. and D. Koss, 3♂ (RWB), Gila National Monument, W. Fork Gila R., 17/V/1974, M. and E. Cather, 3♂, 2♀ (BS); Grant Co., E. Fork Gila R., N. of Junct. with W. Fork, 16/V/1976, W. L. Minckley and D. Bruns, 7♂, 5♀ (WR), Hwy. 15, Gila R., 17/V/1974, M. and E. Cather, 16♂, 12♀, 3 nymphs (BS); Lincoln Co., 1/2 mi. above Bonito Lake, Rio Bonito R., 19/VI/1965, R. W. Baumann, 2♂, 2♀, 14 nymphs (RWB); Rio Arriba Co., San Juan R., 7/VIII/1960, Collector ?, 7♂, 5♀ (SJ). OREGON: Benton Co., 9 mi. N. of Corvallis, Berry Crk., 30/VII/1960, Collector ?, 2♂, 2♀ (SJ), Corvallis, Oak Crk., 21/IV/1935, W. M. W., 1♀ (INHS); Clackamas Co., Molalla, Molalla R., 1/VII/1935, S. G. Jewett, 1♀ (INHS); Deschutes Co., Lapine, Little Deschutes R., 13/VII/1948, S. G. Jewett, 3♂, 2♀ (LCMNH); Harney Co., Frenchglen, Blitzen R., 11/VII/1935, S. G. Jewett, 6♂, 3♀ (LCMNH); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 1-3/VII/1951, B. Malin, 6♂, 4♀ (UU), Crooked Crk., 8/VII/1940, F. Glover, 4♂, 4♀ (RWB), Klamath Falls, ?/VII/1953, J. Schuh, 1♂ (OSU[2]); Malheur Co., Trout Crk., 30/VII/1937,

S. G. Jewett, 3♂, 1♀ (INHS). UTAH: Carbon Co., Spring Glen, Provo R., 19/VII/1952, A. R. Gaufin, 9♂, 8♀ (UU); Duchesne Co., Duchesne, Duchesne R., 3/VIII/1973, B. P. Stark and R. W. Baumann, 2♂, 3♀ (BS); Morgan Co., Henifer, 15/VIII/1943, G. F. Knowlton and Maddock, 1♂ (INHS); Piute Co., Hwy. 89, N. of Big Rock Candy Mt., Sevier R., 2/VI/1977, S. W. Szczytko and K. W. Stewart, 40 nymphs (reared 8♂, 7♀), (SWS and NTSU); Sevier Co., Big Rock Candy Mt., Sevier R., 15/VII/1963, G. F. Knowlton, 1♂, 2♀ (UU), Big Rock Candy Mt., Sevier R., 13/VII/1961, G. F. Knowlton, 1♂, 5♀ (UU), Elsinore, 22/VII/1937, G. F. Knowlton, 2♀ (INHS), Summit Co., 1 mi. W. of Peoa, Weber R., 28/VII/1973, B. P. Stark, 2♂ (BS); Unitah Co., Hwy. 45, below Bonanza, 25/V/1977, S. W. Szczytko and K. W. Stewart, 11 nymphs (reared 2♂, 6♀), (SWS and NTSU), 4 1/2 mi. N. of Whiterock, Whiterock R., 6/VIII/1975, Collector ?, 1♀ (RWB); Wasatch Co., Heber, 14/VIII/1943, G. F. Knowlton and Maddock, 1♀ (INHS), Charleston, 14/VIII/1943, G. F. Knowlton and Maddock, 1♀ (INHS), Snake Crk., 7/VIII/1975, Sakamoto, 1♂ (RWB), Hwy. 40, Provo R., 20/VII/1972, B. P. Stark, 2♂ (BS); Weber Co., Ogden, 12-14/VII/1960, G. F. Knowlton, 1♂, 5♀ (UU), Ogden, 13&17/VII/1959, G. F. Knowlton, 11♀ (UU). WYOMING: Carbon Co., Riverside, Yellowstone National Park, Madison R., 26/VI/1964, Heaton, 7♂, 11♀ (RWB), Madison R., 2/V/1964, Heaton, 30 nymphs (UU); Lincoln Co., La Barge, Green R., 17/VII/1962, A. V. Nebeker, 1♂, 1♂, (SJ);

Sublette Co., Daniel, Hwy. 189, Horse Crk., 18/VII/1962, Collector ?, 3♂, 3♀ (UU), N.W. of Daniel Hwy. 187, Green R., 19/VII/1962, Collector ?, 1♂, 1♀ (UU), N. of Cora, Willow Crk. 18/VII/ , Collector ?, 1♀ (UU), Daniel, Hwy. 189, Prairie Crk., 18/VII/1962, Collector ?, 2♂, 1♀ (UU), Big Pine, Hwy. 189, S. Piney Crk., 18/VII/1962, Collector ?, 4♂, 3♀ (UU); Teton Co., 1 mi. S. of entrance to Yellowstone National Park, Pole Cat Crk., 27/VI/1964, J. W. Richardson and S. L. Jensen, 4♂, 3♀ (RWB), Hwy. 26, Gros Ventre R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 2 nymphs (UU).

Distribution.-- CANADA: British Columbia; USA: Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, Wyoming (Fig. III).

Diagnosis and Discussion

I. mormona is similar to *I. longiseta*. Males can be distinguished by their shorter stouter paraprocts, aedeagus with tubular apex and expanded lobe, truncate vesicle, spinulae pattern of the 9th tergum, distinct "H" pigment pattern and anterior dark patch on head, and by the evenly suffused brown pigmentation of the pronotum. Females can be distinguished by the shallow subgenital plate, and pigmentation patterns described above. Nymphs can be separated by the darker pigmentation of the head and pronotum, long hairs only at lower angles and posterior margin of the pronotum, longer dorsal fringe of hairs on the tarsus, and by the continuous dorsal fringe of long hairs on the cerci after the 16th segment. Ova can be distinguished by the deeper chorionic punctations, slightly raised ridges, and the non-elevated micropyles.

Knight and Gaufin (1966) reported that *I. mormona* was a stenothermic stonefly limited to low altitudes. No studies on the life history or biology have been done on this species. Material examined indicates that emergence begins about the middle of May in southern latitudes and continues until mid-Aug., with peak emergence probably occurring mid-Jul.

Isoperla quinquepunctata (Banks)

Chloroperla quinquepunctata Banks, 1902, 34:124. Holotype ♀; Gallinas R., Las Vegas, New Mexico, USA, (MCZ #11,337).

Isoperla quinquepunctata, Banks, 1906b, 17:175.

Isoperla quinquepunctata, Banks, 1907a:13.

Isoperla quinquepunctata, Claassen, 1940, 232:204.

Isoperla patricia Frison, 1942:313. Holotype ♂, and allotype, Spearfish, Spearfish R., Lawerence Co., South Dakota, (INHS).

NEW SYNONYMY:

Perliola quinquepunctata, Banks, 1947, 54:284.

Isoperla patricia, Illies, 1966:415.

Isoperla quinquepunctata, Illies, 1966:416.

Isoperla patricia, Zwick, 1973:249.

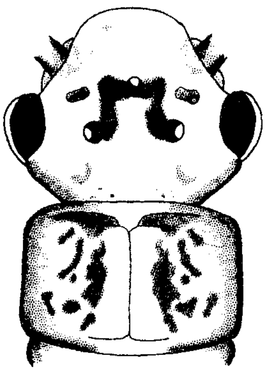
Isoperla quinquepunctata, Zwick, 1973:250.

Additional references: Isoperla quinquepunctata, Seemann, 1927 (nymphal description, no illustrations); Needham and Claassen, 1925 (male and female genitalia); Dodds and Hisaw, 1925; Muttkowski, 1929, Claassen, 1931 (nymphal description, no illustrations); Banks, 1947 (wing, adult maxillary palpus, and ocellar area); Gaufin, 1955; Jewett, 1960; Gaufin et al., 1966 (male and female genitalia); Stewart et al., 1974; Baumann et al., 1977 (male and female genitalia). Isoperla patricia, Frison, 1942 (adult head and pronotum, male and female genitalia, aedeagus, nymphal mandibles, maxillae, labium, and habitus); Ricker, 1943, 1946; Gaufin, 1955; Jewett, 1959, 1960 (nymphal labium, male and female genitalia); Gaufin and Jensen, 1961; Gaufin, 1964b; Knight et al., 1965a (ova); Nebeker and Gaufin, 1966a; Gaufin et al., 1966 (male and female genitalia); Gaufin et al., 1972 (male and female genitalia); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Description (Plates II and IV)

Male (Pl. IV).-- Macropterous-brachypterous. Length of forewings (macropterous) 7-9 mm; length of body 8-10 mm; length of forewings (brachypterous) 3-4 mm; length of

Plate IV. Figs. 1-8. _I. quinquepunctata_. 1. adult head and pronotum (scale: 1 mm = .08 mm). 2. male terminalia, dorsal aspect (1 mm = .04 mm). 3. nymph head and pronotum (1 mm = .09 mm). 4. male vesicle and 8th sternum (1 mm = .04 mm). 5. male paraproct, lateral aspect (1 mm = .02 mm). 6. male vesicle variation (1 mm = .04 mm). 7. male aedeagus, lateral aspect, A. posteroventral band of stout spinulae, B. mesolateral lobe bearing scattered fine spinulae, C. dense band of short stout spinulae, D. small posterior lobe devoid of spinulae, E. posterior conical lobe (1 mm = .02 mm). 8. female subgenital plate (1 mm = .04 mm).



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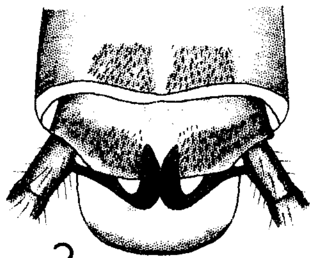

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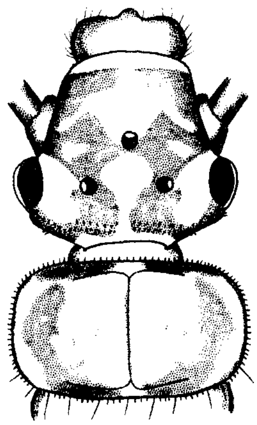

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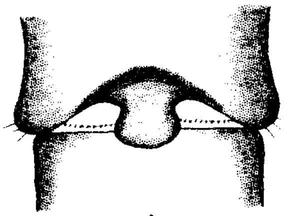

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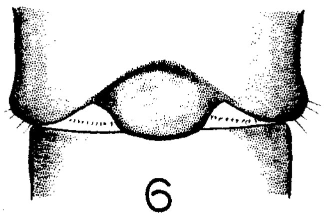

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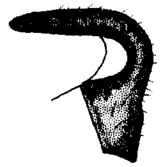

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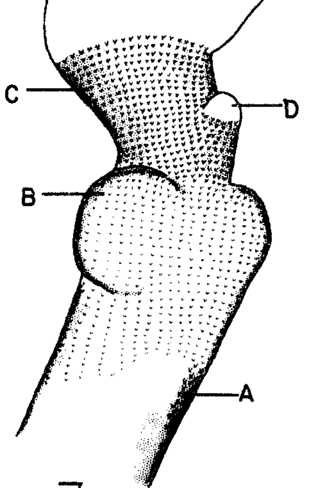

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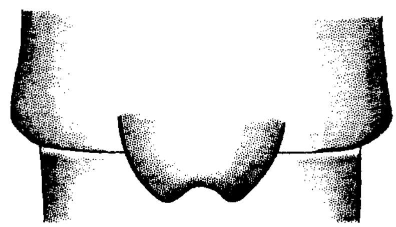

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body 8-10 mm. General body color light brown, often with reddish brown abdomen. Meso-and metathorax dark brown at posterior half. Lateral ocelli connected to anterior ocellus by "r-shaped" band of dark brown pigmentation; 2 dark spots lateral to anterior ocellus. Interocellar area light yellow. Pronotum with dark brown rugosities, and median light yellow stripe (Fig. 1). Ninth and 10th terga with median light furrow, and bipartite patches of long hair-like setae (area of patches sometimes reduced or absent), (Fig. 2). Abdominal terga with patches of long stout hairs at lateral posterior margins. Paraprocts long, curving inward, meeting medially, tapering apically to points and recurving anteriorly over 1/4 10th tergum (Figs. 2 & 5). Vesicle, rounded posteriorly, broader at base than apex (Fig. 6) (sometimes constricted at middle, Fig. 4), base with narrow band of dark pigmentation (Figs. 4 & 6). Aedeagus entirely membranous with 2 mesal, anterolateral lobes covered with small fine spinulae (Fig. 7B) and small posterior lobe with membranous tip void of spinulae (Fig. 7D), apex wider, truncate, void of spinulae and bearing posterior pointed conical lobe (Fig. 7E), heavy band of short, stout spinulae encircling aedeagus above mesal lobes (Fig. 7C), band of finer spinulae encircling aedeagus mesally (Fig. 7B); ventral posterior margin with short band of stout spinulae (Fig. 7A).

<u>Female</u> (Pl. IV).-- Macropterous. Length of forewings

9-11 mm; length of body 9-11 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate variable (see Frison, 1942:313), but generally triangular, produced posteriorly 1/4 the length of 9th sternum, notched at apex, and darker than rest of segment (Fig. 8).

Nymph (Reared), (Pl. IV).-- Length of mature nymph 9-13 mm. Dorsum of head with light brown, quadrangular areas connecting lateral ocelli with anterior ocellus, 1 light spot near base of each lateral ocellus with posterior margin. Interocellar area light with narrow band extending back to occiput. Faint occipital ridge, with sparse, small spinulae on back of head (Fig. 3). Pronotum fringed with evenly spaced small stout hairs; long hairs interspersed at posterior angles and margin; dorsum mostly light except for 2 light lateral brown bands, rugosites absent (Fig. 3). Abdominal terga with 3 longitudinal stripes, 2 lateral and 1 mesal. Femora and tibiae with heavy fringe of long dorsal hairs, tarsi with sparse row of long fine hairs. Posterior margin of cercal segments encircled by whorl of small stout hairs; incomplete dorsal fringe of long fine hairs on segment 16; continual dorsal fringe on 17th and remaining segments.

Ova (Pl. II).-- General shape oval, cross section of anterior 1/2 triangular, cross section posterior 1/2 round (Fig. 6). Color medium brown. Length .24 mm; width .19 mm.

Collar well developed, raised .02 mm from chorion (Figs. 5 & 8). Chorion covered with numerous evenly spaced punctations, ridges produced slightly (Figs. 3 & 6). Micropyles arranged in threes near bottom 1/3, on one side (Figs. 3 & 5).

Material examined.-- TYPES: *I. quinquepunctata*, Holotype ♀, NEW MEXICO: San Miguel Co., Las Vegas, Gallinas R., 9/VI/?, Cockerell, #11,337 (MCZ). Paratypes, *I. patricia*; UTAH: Cache Co., Paradise, 14/VI/1938, Hardy and Stains, 1♂, 11♀ (INHS), Logan Canyon, 11/VII/1938, D. E. and A. T. Hardy, 1♀ (INHS). Additional specimens - CANADA - BRITISH COLUMBIA: Prince George, Nechako R., 13-15/VII/1938, W. E. Ricker, 1♀, 1♀, 1 nymph (INHS). USA - CALIFORNIA: Mono Co., near Crestview, Big Spring, 17/VI/1960, S. G. Jewett, 9♂, 8♀ (SJ); Tehama Co., near Red Bluff, Sacremento R., 31/VII/1965, S. G. Jewett, 3♂ (USNM), near Red Bluff, Sacremento R., 12/IV/1960, S. G. Jewett, 1♂, 2♀, and exuvia (SJ). COLORADO: Archuletta Co., Piedra R., 8/VII/1960, A. R. Gaufin, 4♂, 2♀, 6 nymphs (RWB); Boulder Co., near Boulder, St. Uroin R., 24/VII/1960, A. R. Gaufin, 12♂, 15♀ (UU); Conejos Co., 3 mi. S. of La Manga Pass, Hwy. 17, Los Pinos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 5♂, 10 nymphs (SWS & NTSU), 3 mi. E. of La Manga Pass, Correjos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 3♂ (SWS & NTSU); Douglas Co., West Crk., 11/VIII/1958, 1♂, 1♀, J. A. and H. H. Ross (RWB); Eagle

Co., 42 mi. E. of Glenwood Springs, Eagle R., 10/V/1976, S. W. Szczytko and K. W. Stewart, 3♂ (SWS & NTSU); Fremont Co., 2 mi. W. of Coaldale, Arkansas R., 30/VI/1974, S. J. Herman, 2♂, 1♀ (RWB); Garfield Co., Glenwood Springs, Roaring Fork R., 13/VII/1961, A. R. Gaufin, 22♂, 17♀ (UU); Grand Co., 3 mi. W. of Granby, Colorado R., 20/VI/1961, A. R. Gaufin, 50 nymphs (UU), W. of Granby, Hwy. 40, Colorado R., 27/VI/1962, A. R. Gaufin, 1♀ (UU), 4 mi. W. of Granby, Colorado R., 24/VIII/1960, A. R. Gaufin, 10♂, 8♀ (UU), W. of Granby, Hwy. 40, Colorado R., 27/VI/1962, A. R. Gaufin, 10♀ (UU); Granite Co., Hwy. 50, Arkansas R., 12/VII/1961, Collector ?, 18♂, 20♀ (UU), Arkansas R., 12/VII/1961, Collector ?, 1♂ (UU); Gunnison Co., above Hwy. 50, Soap Crk., 1/VII/1962, A. R. Gaufin, 12♂, 15♀ (UU), Gunnison R. at junct. with Beaver Crk., 7/VI/1961, Collector ?, 8 nymphs (UU), Cebolla Crk. at Powderhorn bridge, 18/VI/1962, Collector ?, 15 nymphs (UU), Beaver Crk. above junct. with Gunnison R., 4/VII/1964, Collector ?, 5 nymphs (UU), Soap Crk. at junct. with Gunnison R., 1/VII/1961, Collector ?, 3♂, 1♀ (UU), Soap Crk. at junct. with Gunnison R., 19/IV/1962, A. R. Gaufin, 25 nymphs (UU), W. Elk Crk., 3/VII/1961, A. R. Gaufin, 15 nymphs (UU), below Sargents, Hwy. 50, Tomichi Crk., 12/VII/1962, A. R. Gaufin, 10 nymphs (UU), Hwy. 114, Cochetopa Crk., 12/VII/1962, A. R. Gaufin, 1♂, 1♀, 15 nymphs (UU), W. Elk Crk. at junct. with Gunnison R., 3/VII/1961, Collector ?, 3♀ (UU); Huerfano Co., 2 mi. E.

of La Veta Pass, Hwy. 160, 6/V/1976, S. W. Szczytko and K. W. Stewart, 3♂, 2♀, 2 nymphs (SWS & NTSU), 1 mi. W. of La Veta Pass, Hwy. 160, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2♂, 1♀, 3 nymphs (SWS & NTSU); Jackson Co., S.W. of Walden, Hwy. 14, Grizzly Crk., 9/V/1976, S. W. Szczytko and K. W. Stewart, 2♂, 1♀ (SWS & NTSU); Mesa Co., Grand Junction, Colorado R., 1/VI/1961, A. R. Gaufin, 2 nymphs (UU), 2 mi. S.E. of De Beque, Colorado R., 11/VIII/1973, B. P. Stark and R. W. Baumann, 1♀ (BS); Moffat Co., Dinosaur National Monument, Pool Crk., 25/VII/1962, D. W. Anderson, 3 nymphs (UU), 4 mi. S.W. of Craig, Hwy. 13, Yampa R., 3/VII/1974, B. P. Stark, 6♂, 2♀ (BS); Montezuma Co., Mancos, Chicken Crk., 8/VII/1960, A. R. Gaufin, 1♂, 1♀ (RWB); Montrose Co., Hwy. 50, Cimarron Crk., 20/IV/1962, A. R. Gaufin, 6 nymphs (UU), 13 mi. above Montrose, Uncompahgre R., 14/VII/1962, A. R. Gaufin, 1♂ (UU); Ouray Co., Hwy. 550, Cow Crk., 15/VII/1962, A. R. Gaufin, 2 nymphs (UU); Park Co., Hartzel, S. Platte R., 18/VIII/1938, J. A. and H. H. Ross, 3♂, 1♀ (INHS); Pitkin Co., S. of Carbondale, Hwy. 133, Crystal R., 10/V/1976, S. W. Szczytko and K. W. Stewart, 3 nymphs (SWS & NTSU); Rio Blanco Co., 2 mi. N. of Meeker, White R., 22/VI/1961, Collector ?, 8 nymphs (UU), Hwy. 5, Piceance Crk., 25/V/1977, S. W. Szczytko and K. W. Stewart, 25 nymphs (reared 8♂, 4♀), (SWS & NTSU), 2 mi. N. of Meeker, White R., 22/VI/1961, A. R. Gaufin, 2♀ (UU), Piceance Crk., 15/VI/1976, L. Grey, 15♂, 11♀, 8 nymphs (CSU);

Routt Co., Hideaway, Yampa R., 29/VI/1968, B. R. Oblad, 6♂, 3♀ (RWB), Soda Crk., 16/VII/1968, B. R. Oblad, 1♂ (UU), E. Fork Elk R., 18/VII/1968, B. R. Oblad, 3♂, 1♀ (UU), Yampa R., 15/VII/1968, B. R. Oblad, 10♂, 20♀, (UU), Steamboat Springs, Yampa R., 25/VI/1962, A. R. Gaufin, 5♂, 6♀ (UU), Yampa R., 16/VII/1968, B. R. Oblad, 28♀ (UU), Focus Ranch, Little Snake R., 17/VII/1968, B. R. Oblad, 2♂, 1♀ (UU), 1 mi. W. of Hayden, Yampa R., 18/VII/1968, B. R. Oblad, 2♂, 11♀ (UU); Saquache Co., Sargents, Tomichi Crk., 11/VII/1961, A. R.Gaufin, 10 nymphs (UU); San Juan Co., Silverton, ?/VII/?, Oslay, 1♂ (CU); San Miguel Co., 3 mi. N. of Placerville, Hwy. 62, Leporad Crk., 11/V/1976, S. W. Szczytko and K. W. Stewart, 8♂, 3♀ (SWS & NTSU).
IDAHO: Bear Lake Co., 1/2 mi. N. of Geneva, Hwy. 89, Thomas Fork Crk., 29/VI/1964, J. W. Richardson and S. L. Jensen, 4♂, 6♀, 30 nymphs (UU); Custer Co., N. of Challis, Salmon R., 19/VI/1963, A. R. Gaufin, 3♂, 9♀ (RWB); Franklin Co., 4 mi. N. of Preston, Hwy. 34, Bear R., 20/VI/1964, J. W. Richardson and S. L. Jensen, 3♂, 9♀ (UU), near Preston, Glendale Reservoir, 24/IV/1952, Collector ?, 1 nymph (UU); Fremont Co., 5 mi. S. of Island Park Reservoir, Henry's Fork, Snake R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 3♂, 5♀ (UU), St.Anthony, Henry's Fork of Snake R., 19/VI/1955, S. G. Jewett, 1♂, 1♀ (UU), 2 mi. N. of Ashton, Hwy. 191, Warm R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 4 nymphs (UU), Mack's Inn, Hwy. 191,

Henry's Fork Snake R., 24/VI/1964, J. W. Richardson and S. L. Jensen, 74 nymphs (UU); Jefferson Co., 1 mi. E. of Ririe, Hwy. 26, Birch Crk., 21/VI/1964, J. W. Richardson and S. L. Jensen, 2 nymphs (UU); Lemhi Co., N. Fork Salmon R., 16/VI/1965, A. R. Gaufin, 47♂, 60♀ (UU), S. of North Fork, Hwy. 93, Wagonhammer Spring, 17/VI/1965, A. R. Gaufin, 1♀ (UU), Ellis, Salmon R., 17/VIII/1963, A. R. Gaufin, 1♂ (UU), N. of Salmon, Salmon R., 19/VI/1963, A. R. Gaufin, 1♀ (UU), 8 mi. S.W. of Shoup, Garden Crk., 4-6/VII/1969, C. R. Whitt, 1♀ (UU). MONTANA: Beaverhead Co., 5 mi. N.E. of Dillon, Beaverhead R., 6/VIII/1966, J. R. Grierson, 1♂, 1♀ (UU); Big Horn Co., 3 mi. W. of Wyola, Big Horn R., 22/VII/1966, J. R. Grierson, 2♂ (UU); Broadwater Co., Toston, Missouri R., 22/VI/1940, J. A. and H. H. Ross, 1♀ (INHS); Carbon Co., Barron Crk., 19/VI/1969, T. Dodson, 2♂, 2♀ (UU), 10 mi. above Yellowstone R., Clark's Fork of Yellowstone R., 25/VI/1966, J. R. Grierson, 4♂, 6♀ (UU); Cascade Co., at Sun R., Hwy. 20, Sun R., 24/VI/1965, A. V. Nebeker, 1♂ (UU); Fergus Co., 2 mi. E. of Lewistown, Spring Crk., 5/VII/1966, J. R. Grierson, 11♂, 13♀ (UU); Flathead Co., Glacier National Park, Bowman Crk., 24/VII/1970, A. R. Gaufin, 15♂, 10♀ (UU), Glacier National Park, N. Fork Flathead R., 14/VII/1967, A. R. Gaufin, 3♂, 11♀ (UU); Glacier National Park, Kintla Crk., 23/VII/1970, A. R. Gaufin, 6♀ (UU); Glacier Co., Glen's Lake, Crk. at outlet, 4/VII/1970, C. Yarmoloy, 2♀ (UU), Glacier National Park, Swift Current Lake, 11/VII/1964, A. R. Gaufin, 2♂ (UU), Glacier National Park, St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 2♂, 2♀ (UU); Gallatin Co., W. Gallatin R., 9/VIII/1951, R. Hays, 3♂, 1♀ (CU); Judith Basin Co., 13 mi. N.E. of Geyser, Arrow Crk., 7/VII/1966, J. R. Grierson, 1♀ (UU); Lake Co., Condon, Swan R., 28/VI/1969, P. Milam, 6♂, 7♀ (UU); Lincoln Co., Hwy. 37, Kootenoi R., 4/VII/1968, 40♂, 38♀ (UU); Meagher Co., Martinsdale, S. Fork of Mussel Shell R., 1/VII/1966, J. R. Grierson, 2♂, 1♀ (UU), Cottonwood Crk., 1/VII/1966, J. R. Grierson, 1♀ (UU); Missoula Co., Alva Lake outlet, Clearwater R., 20/VI/1969, R. L. Newell, 10♀ (UU), Hwy. 20, Blackfoot R., 8/VII/1964, A. R. Gaufin, 10♂, 18♀ (UU), 16 mi. above Hwy. 93, Lolo R., 16/VII/1965, J. R. Grierson, 1♂ (UU), Swan Valley, Hwy. 209, Morrel Crk., 8/VII/1964, A. R. Gaufin, 1♂ (UU); Park Co., 7 mi. above Yellowstone R., Shields R., 1/VII/1966, J. R. Grierson, 3♂, 5♀ (UU), Livingstone, Yellowstone R., 3/VII/1938, Forsyth and Platsch, 1♀ (UU); Ravalli Co., N. of Hamilton, Hwy. 93, Bitterroot R., 23/VII/1965, J. R. Grierson, 3♂, 4♀ (UU), Ravalli, Hwy. 93, Jocko R., 30/VI/1963, A. R. Gaufin, 1♂, 3♀ (UU); Stillwater Co., Columbus, Yellowstone R., 25/VI/1966, J. R. Grierson, 2♂ (UU); Sweetgrass Co., Big Timber, Yellowstone R., 30/IV/1966, J. R. Grierson, 35♂, 37♀ (RWB). NEVADA: Clark Co., 5 mi. N. of Paradise Valley, Martin Crk., 18/VI/1967, D. M. Lehmkulh, 2♂, 4♀

(RWB); White Pine Co., Lehman Caves National Monument, 30/VI/1939, Thacker, 1♂, 1♀ (SJ). NEW MEXICO: Colfax Co., 6 mi. N.W. of Cimarron, Hwy. 64, 9/VI/1954, R. L. Wenzel, 1♂, 3♀ (SJ); Rio Arriba Co., San Juan R., 4/VII/1966, A. R. Gaufin, 1♂, 1♀ (RWB), 15 mi. N.W. of Tres Piedras, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 3♂, 7♀ (SWS & NTSU), S. of Chama, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 1♂, 3♀, 6 nymphs (SWS & NTSU); San Miguel Co., Las Vegas, Date ?, H. S. Barber, 1♀ (SJ), above Pecos, Hwy. 63, Pecos R., 4/VI/1977, S. W. Szczytko and K. W. Stewart, 2♂, 1♀, 3 nymphs (SWS & NTSU); Santa Fe Co., Santa Fe, 22/VI/1949, D. G. Denning, 1♂, 1♀ (SJ); Taos Co., 8 mi. W. of Ute Park, Hwy. 64, 7/V/1976, S. W. Szczytko and K. W. Stewart, 3♂, 2♀, 8 nymphs (SWS & NTSU). OREGON: Clatsop Co., 2 mi. E. Elsie, Nebalem R., 11/VII/1964, S. G. Jewett, 5♂, 3♀ (SJ), 4 mi. N.E. Elsie, Red Bluff, Nebalem R., 12/V/1965, S. G. Jewett, 2♂, 2♀ (CU); Deschutes Co., Tumalo Reservoir, 24/VI/1954, H. H. Ross, 1♀ (INHS); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 1-3/VII/1951, B. Malkin, 4♂, 3♀ (UU); Lane Co., Willamette R., 25/VI/1946, S. G. Jewett, 8♀ (LCMNH), 15 mi. N. Lakeview, Crooked R., 7/VI/1955, R. Schuh, 1♂ (OSU[2]). SOUTH DAKOTA: Custer Co., Custer State Park., Iron Crk., 6/VII/1968, Harris and Cooley, 2♀, 1 nymph (RWB); Lawerence Co., Black Hills National Park, near Savoy, Rt. 14, 6/VII/1968, Harris and Cooley, 3♂, 4♀, 1 nymph (RWB), Spearfish, 27/VII/1940, T. H. and T. H. Frison, Jr., 2♀, 1 nymph (INHS). UTAH: Cache Co., Paradise, 14/VI/1938, Hardy and Stains, 1♂, 11♀ (INHS); Duchesne Co., Duchesne, Duchesne R., 3/VIII/1973, B. P. Stark and R. W. Baumann, 1♀ (BS); Emery Co., Stewart Station, 10/V/1975, Collector ?, 1♀ (RWB); Garfield Co., 3 mi. E. of Panguitch Lake, 12/VII/1961, G. F. Knowlton, 4♂, 10♀ (UU); Millard Co., Kanosh Canyon, 12/VIII/1946, G. F. Knowlton, 2♂, 3♀ (RWB), Kanosh Canyon, 27/V/1939, G. F. Knowlton and Harmston, 1♂, 1♀ (INHS), Maple Hollow Forest Camp, 11/VI/1959, Collector ?, 1♀ (UU), Kanosh Canyon, 1/VI/1977, S. W. Szczytko and K. W. Stewart, 20♂, 30♀, 21 nymphs (reared 8♂, 11♀), (SWS & NTSU); Rich Co., above Randolph, Big Crk., 21/VIII/1975, Reichert, 2♂, 7♀ (RWB); Salt Lake Co., Big Cottonwood Crk., 29/V/1953, G. F. Edmunds, 20 nymphs (RWB); Butterfield Canyon Crk., 1/VI/1977, S. W. Szczytko and K. W. Stewart, 48 nymphs (reared 21♂, 12♀), (SWS & NTSU); San Juan Co., Manti La Sue National Forest, Pack Crk., 12/V/1976, S. W. Szczytko and K. W. Stewart, 38 nymphs (reared 10♂, 8♀), (SWS & NTSU); Sevier Co., W. of Sevier, Hwy. 4, Clear Crk., 1/VI/1977, S. W. Szczytko and K. W. Stewart, 18♂, 23♀, 30 nymphs (SWS & NTSU); Summit Co., 1 mi. W. of Peoa, Weber R., 28/VII/1973, B. P. Stark, 3♂, 7♀ (UU), Henefer, 24/VI/1943, G. F. Knowlton, 1♂, 2♀ and exuvia (INHS), Silver Crk., 29/VI/1943, G. F. Knowlton and Telford, 4♂, 3♀ (INHS); Unitah Co., 8 mi. N. of Vernal, 22/VI/1949, I. L. Bell, 1♀ (RWB); Wasatch Co., near Heber, Center Crk., 7/VIII/1975, Sakamoto, 1♂, 3♀ (RWB), Trout Crk., 3/IV/1965, D. C. Hales, 2 nymphs (UU); Weber Co., Ogden Canyon, 18/VI/1938, M. C. Tanner, 1♀ (UU), Weber R., 24/III/1957, G. Smith, 3 nymphs (UU). WYOMING: Lincoln Co., Elbow Forest Camp, Hwy. 89, Snake R., 19/VII/1962, Collector ?, 1♀ (UU), La Barge, Green R., 17/VII/1962, Collector ?, 2♂ (UU), La Barge, Hwy. 189, La Berge Crk., 18/VII/1962, Collector ?, 7♂, 12♀ (UU), Silver Springs, Hwy. 189, Salt R., 19/VII/1962, Collector ?, 14♂, 22♀ (UU); Park Co., Yellowstone National Park, Firehole R., 6/VI/1946, Collector ?, 2♀ (UU); Sublette Co., N.W. of Daniel, Hwy. 187, Green R., 19/VII/1962, Collector ?, 2♀ (UU), Big Piney, Hwy. 189, Cottonwood Crk., 18/VII/1962, Collector ?, 4♂, 2♀ (UU), Pinedale, Pine Crk., 20/VII/1972, B. P. Stark, 1♂ (BS), Daniel, Hwy. 189, Horse Crk., 18/VII/1962, Collector ?, 2♀ (UU), N. of Cora, Willow Crk., 18/VII/1962, Collector ?, 1♀ (UU), N. of Daniel, Hwy. 189, Green R., 18/VII/1962, Collector ?, 6♂, 10♀ (UU); Teton Co., 1 mi. S. of entrance to Yellowstone National Park, Polecat Crk., 27/VI/1964, J. W. Richardson and S. L. Jensen, 1 nymph (UU); Unita Co., Evanston, Bear R., 16/VII/1962, Collector ?, 5♂ (UU), Fort Bridger, Groshen Crk., 21/VII/1967, R. W. Baumann, 1♀ (RWB).

Distribution.-- CANADA: British Columbia. USA: California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, South Dakota, Utah and Wyoming (Fig. III).

Diagnosis and Discussion

I. quinquepunctata is most similar to *I. longiseta*. Males can be distinguished by the broader paraprocts, absence of 2 short finger-like membranous lobes on dorsum of aedeagus, presence of 2 large mesal lobes on aedeagus, and presence of hair-like setae on the 10th tergum. Females can be separated by the narrower deeply notched subgenital plate. Nymphs can be separated by the darker pigment pattern of the head, lack of rugosities on the pronotum, and by the continual dorsal fringe of long hairs after the 17th cercal segment, and absence of long posterior ventral hair. Ova can be distinguished by the triangular-shaped cross section of the anterior 1/2, and the non-elevated micropyles.

I. patricia Frison is placed in synonomy with *I. quinquepunctata* (Banks), based on my extensive holomorphological analysis and behavioral study. Part of the confusion surrounding *I. quinquepunctata* results from the lack of good character illustrations accompanying the original description, and paucity of verified specimens. Prior to my study, the type female was the only confirmed specimen available for comparison.

Two successive collecting trips were made in May, 1976 and Jun., 1977 to the type locality, Gallinas R. near Las Vegas, New Mexico, but no specimens were found. Installation of a dam, intensive irrigation uses, and probable pesticide pollution have drastically altered the ecology of the river since original collections, thereby eradicating or severely reducing populations. Ova from the type I. quinquepunctata female, and other females from the type locality and nearby streams, were compared with those from I. patricia paratypes from the South Dakota type locality and Utah streams. No discernable differences were found in the structure, chorionic sculpturing or micropyle arrangement in these eggs. Also, a comparison of adult genitalia of these specimens revealed no diagnostic character differences.

Study of many I. quinquepunctata aedeagii from diverse localities over its geographic range, revealed no variation in shape, lobation or spinulation. These from the Pecos River, New Mexico (near the type locality) were identical to those from the Black Hills National Monument, South Dakota, near the type locality of I. patricia. No difference was noted in the species specific drumming signals of specimens studied from Colorado, New Mexico and Utah (unpublished concurrent study).

This species exhibits a large amount of morphological variation in male wing length, area of bipartite patches of long hair-like setae on the 9th and 10th terga, shape of vesicle on 9th sternum, shape of female subgenital plate, and general body size. At several localities many variations in these characters could be observed in one population. Males collected and reared from Piceance Crk., Rio Blanco Co., Colorado, were both macropterous and brachypterous, exhibited both vesicle shapes, and displayed variations in the area of setae on the 9th and 10th terga. The subgenital plate of females also exhibited a great amount of variation. No correlation between wing length and any of the variable characters was observed. The most stable diagnostic characters in all populations studies were the male paraprocts, aedeagus, ova, and the drumming signal.

Dodds and Hisaw (1925) reported that *I. quinquepunctata* was distributed between 6,000-9,000' in the Colorado Rockies, and Knight and Gaufin (1966) stated that *I. patricia* was a eurythermic stonefly species found between 6,800-9,400'. Ricker (1964) reported this species was typically distributed in the "eastern foothills and inter-mountain valleys and plateaus, rather than the main ranges" in Canada, and were found in large warm river systems. No studies on the life history of general biology have been done for this species. Based on the material examined emergence begins in early May in southern latitudes and continues until early Aug., with the largest numbers taken from the last of Jun. to the first of Jul.

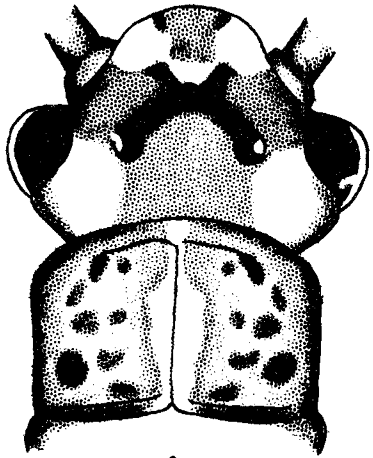
Individual Species (not assigned to group)

Isoperla katmaiensis NEW SPECIES

Description (Plates V and VI)

Male (Pl. V).-- Brachypterous. Length of forewings 5.3 mm; length of body 9.8-11.4 mm. General body color dark brown. Lateral ocelli of head connected to anterior ocellus by narrow black band, interocellar area medium brown, wide medium brown band extending from back of head to anterior ocellus and laterally to base of antennae, anterior frons with medium brown patch (Fig. 1). Pronotum medium brown, variable-width light median stripe, rugosities rounded, dark brown to black (Fig. 1). Wings fumose, veins dark brown. Abdominal terga with 8 rows of longitudinal dots, 2 mesal and 3 each laterally, median rows most prominent. Ninth tergum with bipartite patch of stout spinulae on posterior margin (Fig. 3). Tenth tergum with narrow, light unsclerotized median trough (Fig. 3). Posterior margin of cercal segments with whorl of medium-length hairs and one long dorsal and ventral hair. Vesicle distinctively petiolate, evenly rounded posteriorly, darker than rest of segment, base with narrow dark band extending to lateral margins of segment (Fig. 2). Paraprocts long and stout, tapering to points apically and deflecting outward, curving anteriorly over 1/4 10th tergum, posterior margin with long fine hairs (Figs. 3 & 5). Aedeagus entirely membranous, petiolate, 2 long, tubular, membranous processes at apex (Fig. 4F), dorsal section void of spinulae, large conical lobe on anterior margin void of spinulae (Fig. 4E), large flattened lobe on posterior margin with narrow dorsal patch of long stout spinulae (Fig. 4B & C), one single and one double small posterior finger-like lobes

Plate V, Figs. 1-6. I. katmaiensis. 1. adult head and pronotum (scale: 1 mm = .05 mm). 2. male vesicle and 8th sternum (1 mm = .02 mm). 3. male terminalia, dorsal aspect (1 mm = .02 mm). 4. male aedeagus, lateral aspect, A. proximal stalk bearing concentrated small, stout spinulae, B. large flattened mesoposterior lobe, C. narrow band of long stout spinulae, D. scattered patch of very large stout spinulae, E. large anterior conical lobe, F. long tubular dorsal membranous processes (1 mm = .02 mm). 5. male paraproct, lateral aspect (1 mm = .01 mm). 6. female subgenital plate (1 mm = .05 mm).



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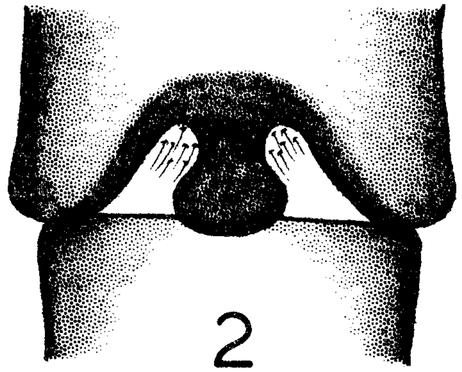

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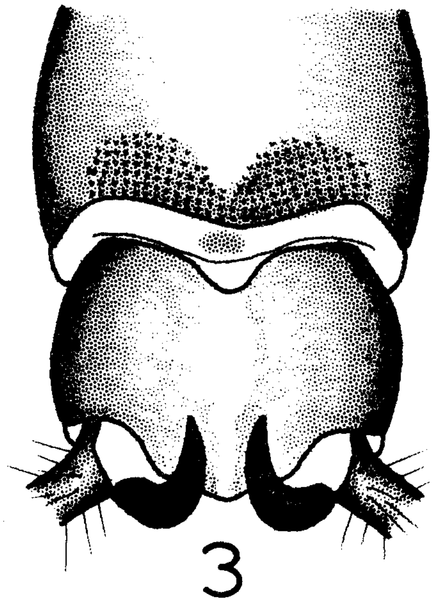

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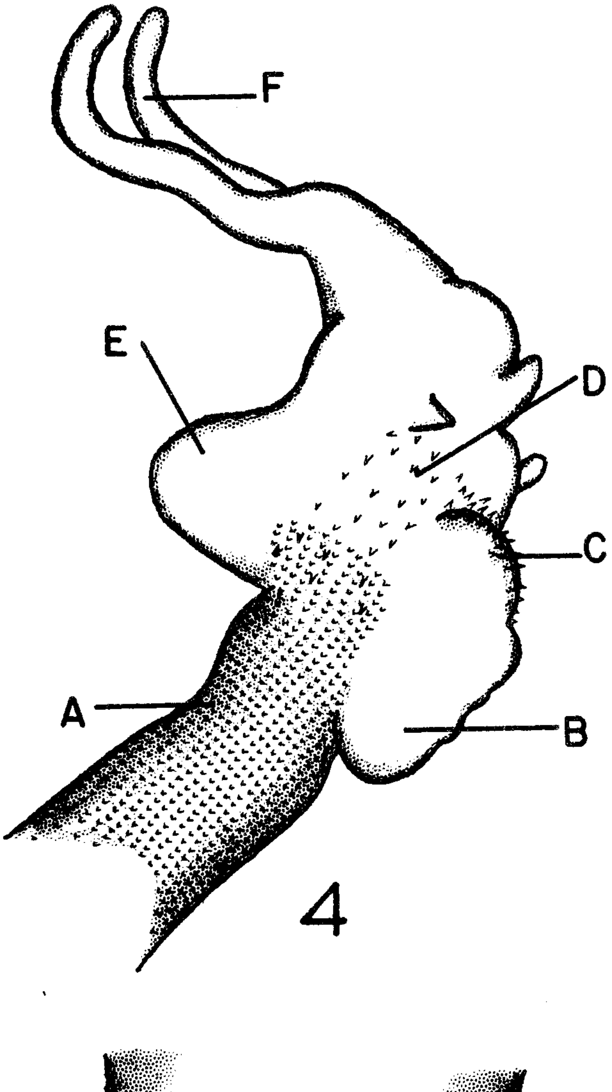

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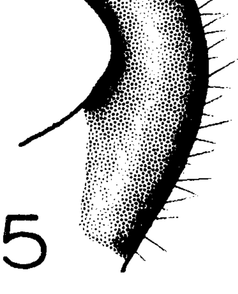

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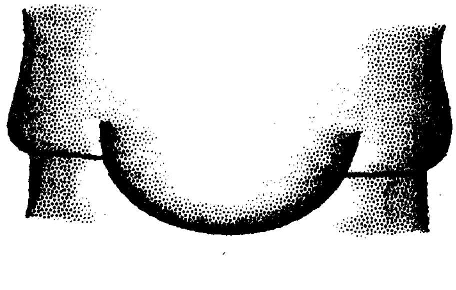

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above large flattened lobe, proximal stalk bearing heavy concentration of small stout spinulae (Fig. 4A), scattered patch of very large stout spinulae on mesal section (Fig. 4D), small triangular lobe above stout spinulae patch.

Nymph.-- UNKNOWN.

Female (Pl. V).-- Macropterous. Length of forewings 13.1-16.1 mm; length of body 11.4-14.3 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate wide at base, semicircular, produced approximately 1/4 length of 9th sternum (Fig. 6).

Ova (Pl. VI).-- General shape oval, cross section circular (Fig. 4). Color dark brown. Length .28 mm; width .20 mm. Collar well developed, ornate, with thickened, elevated irregular ridges forming apical depression (Fig. 6). Chorion entirely smooth. Micropyles arranged in 2 sets of 3 in a row near bottom 1/3 on one side, elevated sperm guides below each micropyle (Figs. 4 & 5).

Material examined.-- TYPES: Holotype ♂, and allotype ♀, USA, ALASKA, Katmai National Monument, Brooks R., at BCF Camp, 4/VII/1969, K. J. Raedeke (RWB), (types deposited at USNM). Paratypes USA, ALASKA, Katmai National Monument, Brooks R., at BCF Camp, K. J. Raedeke (RWB), 18/VI/1969, 5♂, 2♀, 20/VI/1969, 5♂, 1♀, 24/VI/1969, 5♂, 1♀, 4/VII/1969, 10♂, 2♀, 17/VII/1969, 3♂ (paratypes deposited at USNM, RWB, NTSU & SWS).

Distribution.-- USA: Alaska (Fig. IV).

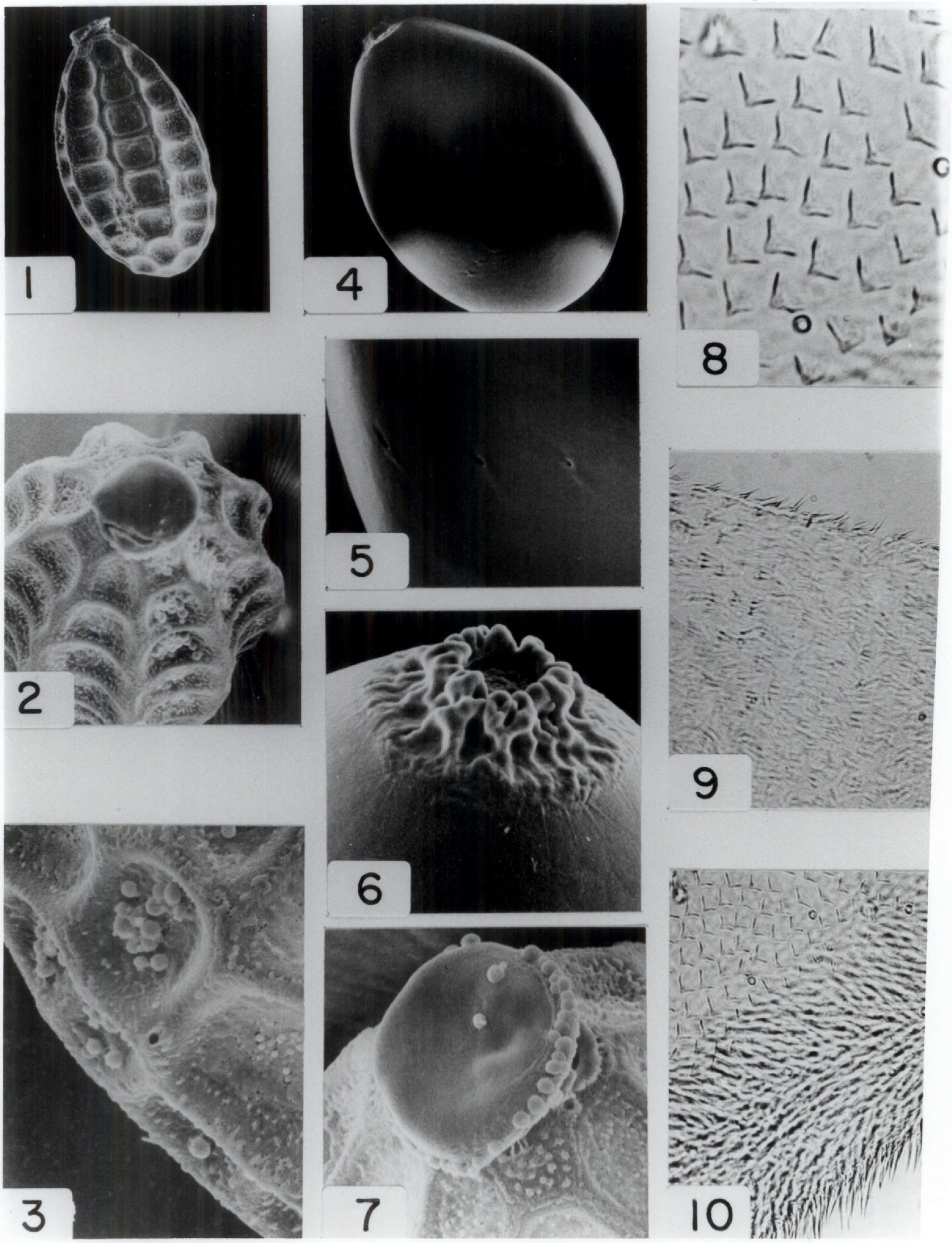
Plate VI. Scanning electron micrographs of *Isoperla*, *Cascadoperla* ova, and light micrographs of aedeagal armature*

Figs. 1-3 & 7. *Cascadoperla trictura*. 1. whole ova 200X. 2. dorsal view of collar and longitudinal ridges 400X. 3. detail of micropyle 1000X. 7. detail of collar 1000X.

Figs. 4-6. *I. katmaiensis*. 4. whole ova 200X. 5. detail of micropyles 700X. 6. detail of collar 700X.

Figs. 8-10. *I. tilasqua*. 8. light micrograph - small stout spinulae on aedeagus 800X. 9. light micrograph - small fine hair-like spinulae on aedeagus 800X. 10. light micrograph - long hair-like spinulae on aedeagus 800X.

* magnifications represent original values before reduction of plate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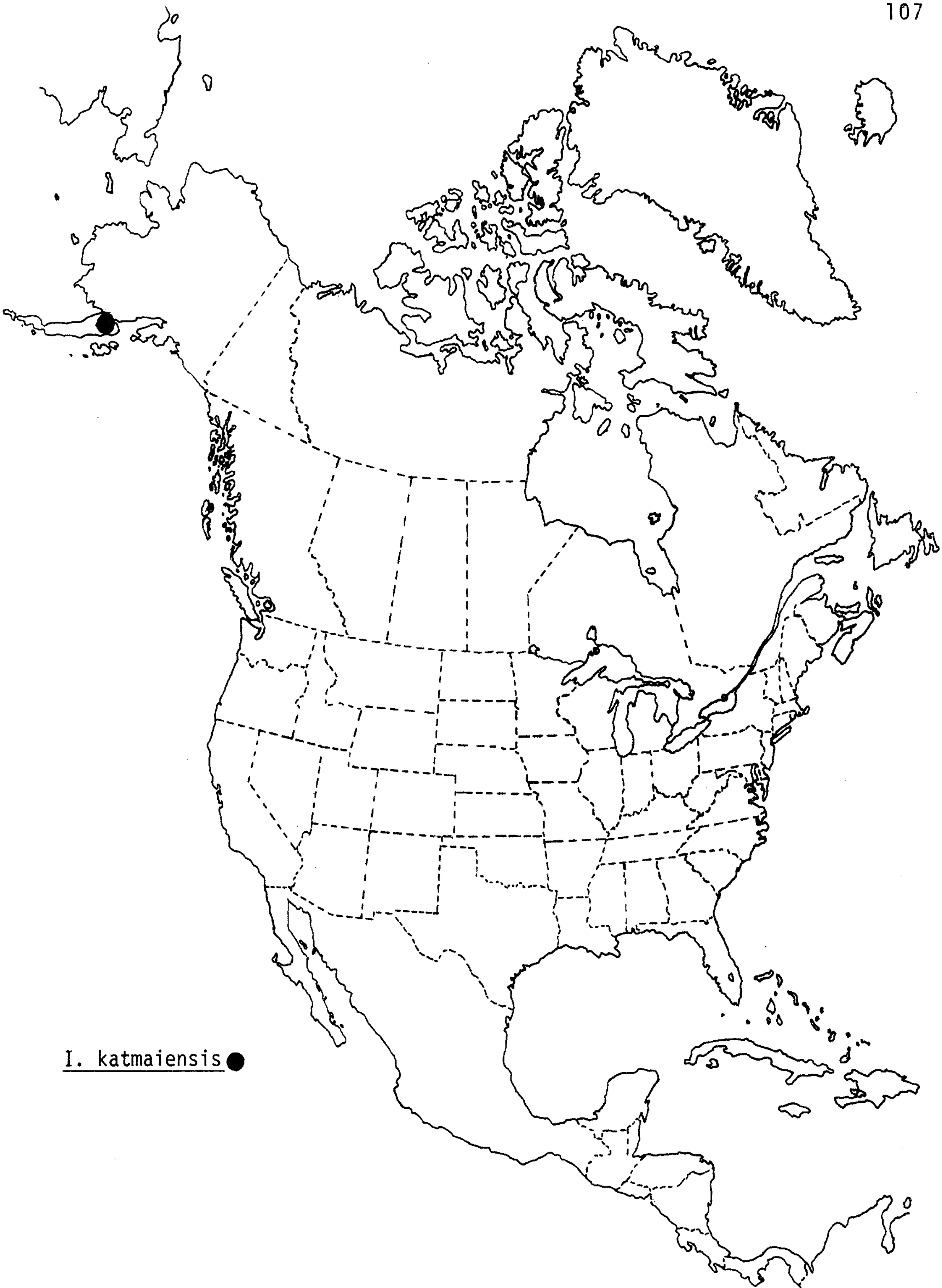
Diagnosis and Discussion

This species is most similar to _I_. _jewetti_. Males can be differentiated by the darker general body color and head-pronotal pigment patterns, absence of two dark brown patches on the 10th tergum, petiolate shape of vesicle, presence of a narrow, light unsclerotized median trough on the 10th tergum, shorter stout paraprocts, presence of 2 long, tubular processes on apex of the aedeagus, and patterns, shapes, and sizes of aedeagul spinulae. Females can be differentiated by the general darker body color and head-pronotal pigment patterns and subgenital plate (in some specimens the subgenital plate is very similar). Ova can be separated by the ornate collar with thickened, elevated, irregular ridges, entirely smooth chorion and lack of chorionic punctations.

This species is not placed in any species group at this time due to the uniqueness of the ova. The ova are unlike any known _Isoperla_ and are similar to some perlid ova. It is closest to the _I_. _quinquepunctata_ complex in that males have an entirely membranous aedeagus and bipartite patch of spinulae on the 9th tergum, and the female subgenital plate is broadly rounded.

This species is apparently rare and restricted to the extreme northern part of the North American Continent (Fig. IV), and probably represents one of the limits of the northwest range of the genus _Isoperla_ in North America.

Fig. IV. Distribution of I. katmaiensis


I. katmaiensis

No data on the life history or general biology are available. Based on the material examined, emergence occurs from mid-Jun. to mid-Jul., and the species occurs in rivers.

Etymology.-- This species is named after the type locality from the Katmai National Monument in Alaska.

Species Group B

Isoperla phalerata complex

This group is composed of *I. phalerata* (Needham) and *I. pinta* Frison. Both species share the following characteristics: 1. male aedeagus entirely membranous, bearing a large patch of small stout spinulae, and many lobes; 2. male 9th tergum with either a single or bipartite patch of stout spinulae; 3. reduced male vesicle; 4. sharply tapered paraprocts with acute ventral spine; 5. broad female subgenital plate, rounded posteriorly with a median notch; 6. contrasting dark brown and yellow head-pronotal pigment patterns in nymph and adult; 7. nymphal pronotum with angles rounded and fringed with small stout setae; 8. nymphal femorae, tibiae, and tarsi with a dorsal fringe of long fine hairs; 9. abdominal terga with 3 longitudinal stripes and 8 longitudinal rows of dots; 10. ova with well-developed collar and chorionic ridges; 12. sculpturing of chorion variable; and 3. micropyles elevated and arranged in pairs or threes near bottom 1/3, on one side.

The group is distributed from South Dakota to California, and New Mexico to Canada (Fig. V). Both species inhabit creeks and small- to medium-sized rivers. Emergence continues from May until the end of Jul., and both species are thought to undergo univoltine life cycles.

Isoperla phalerata (Needham)

Dictyogenus? phaleratus Needham, 1917, 43:485. Holotype ♀; New Mexico, USA (CU #1,151), (wings and female genitalia).

Perla phalerata, Needham and Claassen, 1925, 2:91 (female genitalia and ova).

Perla phalerata, Claassen, 1940, 232:144.

Perliphanes phaleratus, Banks, 1947; 54:278.

Isogenus phaleratus, Ricker, 1952, 18:131 (female head, wings and genitalia).

Isoperla phalerata, Jewett, 1954, 11:548. Allotype ♂, Grand Ronde R., La Grane, Union Co., Oregon (CAS) (male genitalia).

Isoperla phalerata, Illies, 1966:415.

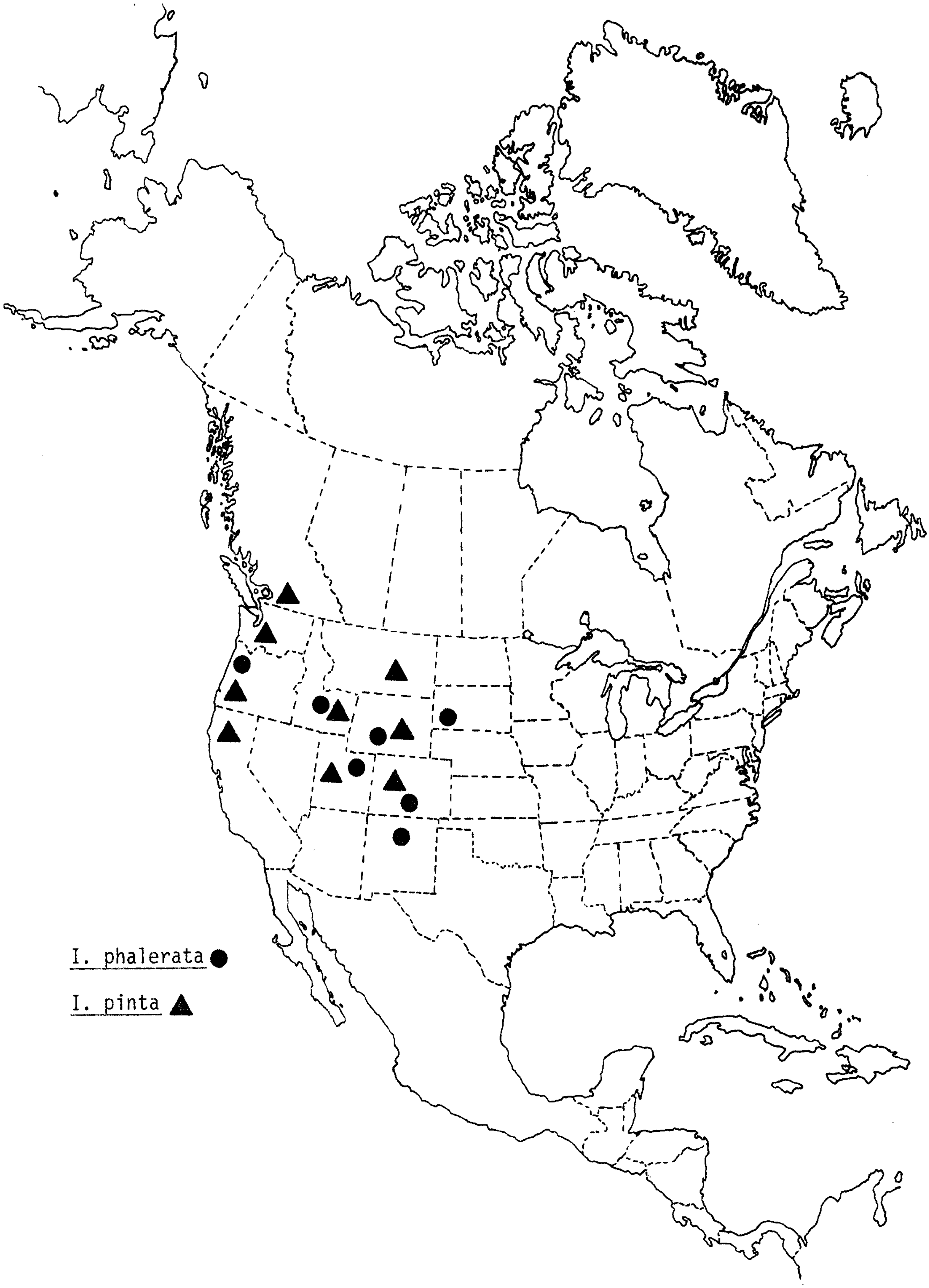
Isoperla phalerata, Zwick, 1973:250.

Additional references: Isoperla phalerata, Jewett, 1959 (male genitalia), Gaufin, 1964b; Logan and Smith, 1966; Stewart et al., 1974; Baumann et al., 1977 (wings).

Description (Plates VII and VIII)

Male (Pl. VII).-- Macropterous-brachypterous. Length of forewings (macropterous) 9-11 mm; length of body 8-11 mm; length of forewings (brachypterous) 5-6 mm; length of body

Fig. V. Distribution of the *I. phalerata* complex

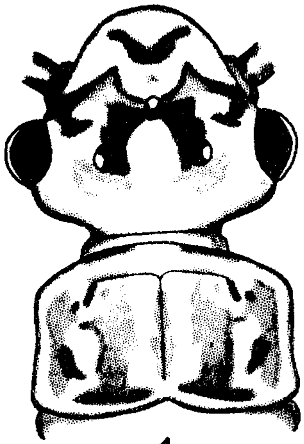

I. phalerata
I. pinta

10-11 mm. General body color medium brown. Head-pronotal pigment pattern with contrasting dark brown and bright yellow areas. Lateral ocelli connected to anterior ocellus by "n"-shaped band of dark brown pigmentation; thin dark "u"-shaped band connecting anterior ocellus with thin dark bands extending from base of antennae; short black bands extending backward from each antennal base; interocellar space light yellow; frons with variable dark band (Fig. 1). Pronotum with median yellow stripe and longitudinal dark brown patches (Fig. I). Cross veins usually present in radial sector of forewings (variable, in one or both wings, or none) (Fig. 5). Ninth tergum with bipartite patches of small stout spinulae at posterior margin; median anterior 1/2 with dark brown patch (Fig. 4). Tenth tergum light yellow with median dark spot (Fig. 4). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts tapering to blunt tips, with acute apical ventral spine (Fig. III); appearing sharp from dorsal view (Fig. 4); recurving anteriorly over 1/4 10th tergum, and deflecting slightly outward; surface bearing small fine hairs (Figs. 3 & 4). Vesicle reduced, not projecting beyond anterior margin of 9th sternum; wider at base than apex; broadly rounded posteriorly; darker than rest of segment (Fig. 2). Aedeagus entirely membranous; one median posterolateral lobe with small, fine scattered spinulae (Fig. 7A); one small posterodorsal, 2 dorsal and l anterodorsal lobes devoid of spinulae (Fig. 7); mesal section covered with dense, small, stout spinulae (Fig. 7B); patch of longer, slender spinulae above stout spinulae at posterodorsal margin, below small anterodorsal lobe (Fig. 7C).

Female (Pl. VII).-- Macropterous. Length of forewings 11-15 mm; length of body 9-12 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, produced 3/8 length of 9th sternum, rounded posteriorly with a slight median emargination (variable, from deeply notched to absent) (Fig. 6).

Nymph (Reared), (Pl. VII).-- Length of mature male nymph 11-14 mm; length of mature female nymph 13-16 mm. Dorsum of head with dark brown transverse pigment band extending between antennal bases; band extended backward to lateral ocelli. Interocellar space light. Occipital ridge, with medium, stout spinulae (Fig. 8). Pronotum fringed with small stout setae, 1 or 2 long hairs irregularly placed; angles broadly rounded (Fig. 8). Abdominal terga with 3 longitudinal stripes, 2 lateral and 1 mesal, and 8 rows of longitudinal dots, 2 mesal and 3 each laterally. Femora with dorsal fringe of long fine hairs; tibiae with dense fringe, and tarsi with less concentrated fringe. Posterior margin of cercal segments with whorl of small stout hairs; incomplete dorsal fringe of medium

Plate VII. Figs. 1-8. *I. phalerata*. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. male vesicle and 8th sternum (1 mm = .06 mm). 3. male paraproct, lateral view (1 mm = .02 mm). 4. male terminalia, dorsal aspect (1 mm = .07 mm). 5. female left forewing, A. radial sector, B. cross veins of radial sector (1 mm = .31 mm). 6. female subgenital plate (1 mm = .08 mm). 7. male aedeagus, lateral aspect, A. mesoposterior lobe bearing small, fine scattered spinulae, B. dense small stout spinulae, C. long slender spinulae, D. anterodorsal lobe (1 mm = .05 mm). 8. nymph head and pronotum (1 mm = .05 mm).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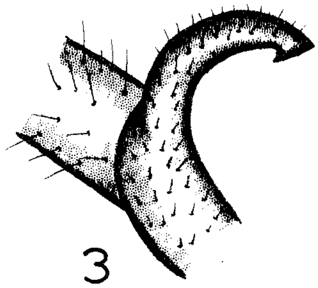
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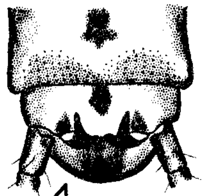
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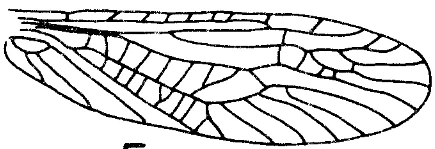
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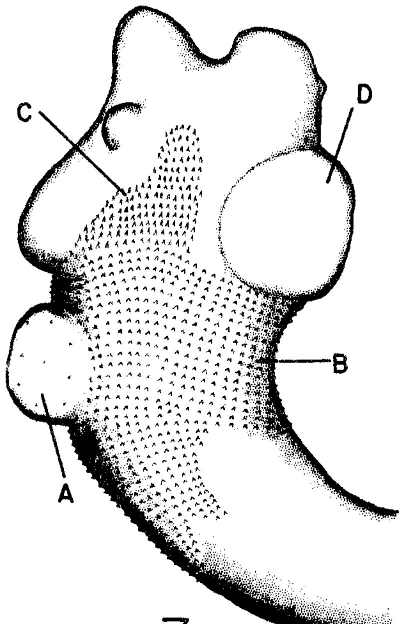

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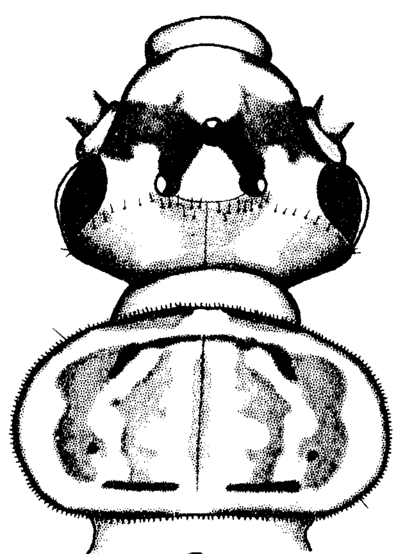
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length hairs on segment 17; continual dorsal fringe on 17th and remaining segments; 1 long ventral hair at posterior margin after 20th segment.

Ova (Pl. VIII).-- General shape oval, cross section circular (Fig. 5). Color light brown. Length .28 mm; width .20 mm. Collar well developed (Figs. 5, 6 & 8). Chorion bearing numerous, evenly spaced punctations, chorionic ridges elevated slightly (Figs. 5 & 6). Micropyles raised with large openings, grouped 3 in a row near bottom 1/3, on one side (Fig. 7).

Material examined.-- TYPES: Holotype ♀, NEW MEXICO: Date ?, Collector ? (CU #1,151). Allotype ♂, OREGON: Union Co., La Grande, Grande Ronde R., 6/VI/1948, D. G. Denning (CAS). Additional specimens - USA: COLORADO: Huerfano Co., Hwy. 160, 2 mi. E. of La Veta Pass, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2♀, 3 nymphs, 1 exuvia (SWS & NTSU); Jackson Co., S.W. of Walden, Hwy. 14, Grizzle Crk., 9/V/1976, S. W. Szczytko and K. W. Stewart, 10 nymphs (reared 3♂), (SWS & NTSU); County ?, Willow Crk. Pass, 2/VII/1962, R. and K Dreisback, 1♀ (WR). IDAHO: Adams Co., 15 mi. N. of New Meadows, Hwy. 95, Little Salmon R., 17/VI/1964, Collector ?, 2♂ (RWB). NEW MEXICO: Colfax Co., Ute Park, Cimarron Canyon, 12/VI/1956, Collector ?, 1♂, 3♀ (WR); Rio Arriba Co., 15 mi. N.W. of Tres Piedras, Hwy. 64, 6/V/1976, S. W. Szczytko and K. W. Stewart, 2♂, 3♀, 3 exuviae (SWS & NTSU). OREGON: Harney Co., Trout

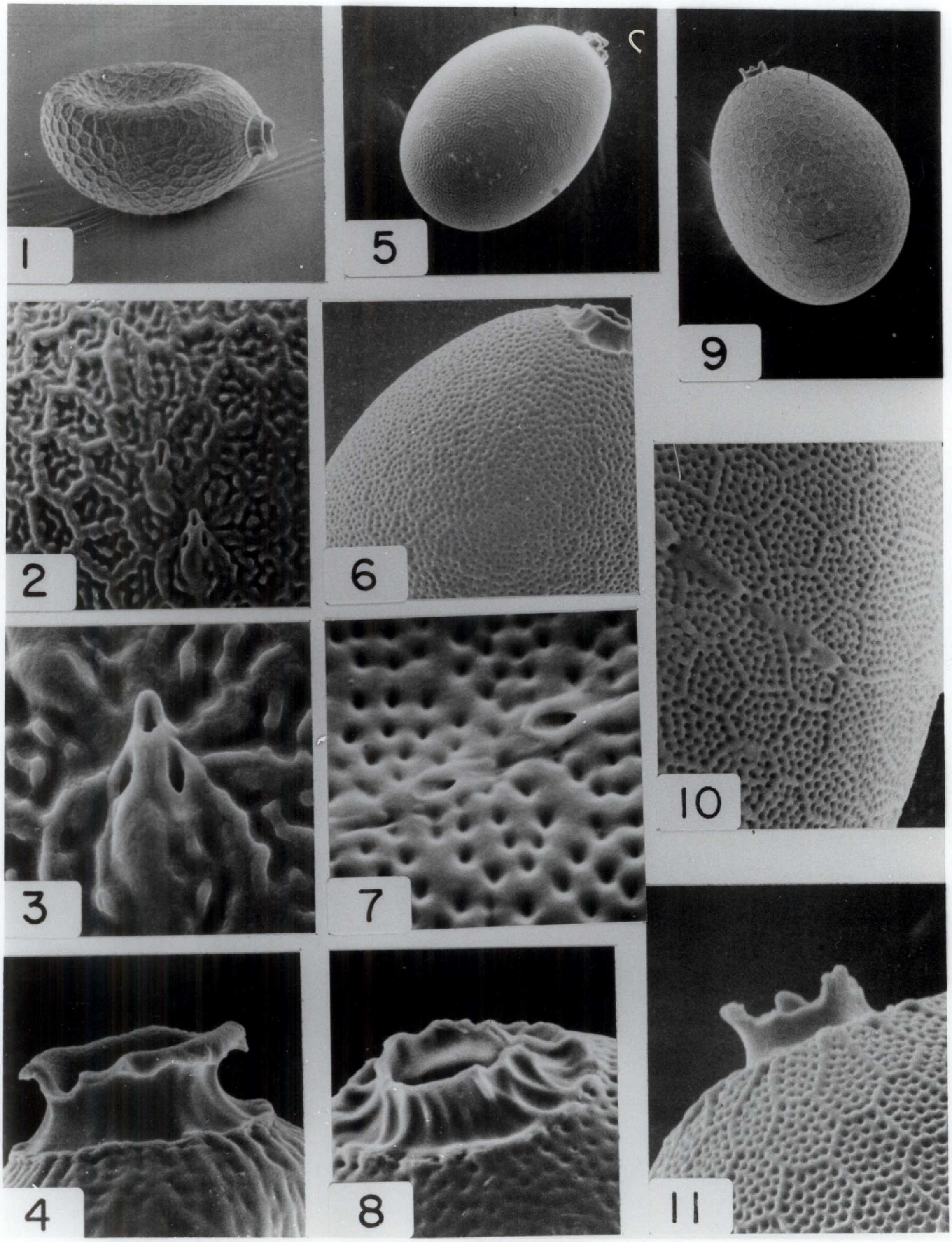
Plate VIII. Scanning electron micrographs of *Isoperla* ova.*

Figs. 1-4. *I. pinta*. 1. whole ova 200X. 2. detail of chorion 700X. 3. detail of ornate micropyle 2000X. 4. detail of collar 1000X.

Figs. 5-8. *I. phalerata*. 5. whole ova 200X. 6. detail of chorion 400X. 7. detail of micropyles 1000X. 8. detail of collar 1000X.

Figs. 9-11. *I. petersoni*. 9. whole ova 200X. 10. detail of chorion and micropyle ridge 1000X. 11. detail of collar 1000X.

* magnifications represent original values before reduction of plates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Crk., 23/V/1950, Fender and S. G. Jewett, 1♂, 2♀ (SJ), Frenchglen, 26/VI/1951, B. Malkin, 2♀ (SJ); Lake Co., Chandler State Park, 27/V/1957, B. Malkin, 2♂ (SJ), Chewaucan R., 18/VI/1955, J. Schuh, 2♂, 4♀ (SJ). UTAH: Garfield Co., Panguitch Crk., 27/VI/1967, G. F. Knowlton, 2♀ (WR).

Distribution.-- USA: Colorado, Idaho, New Mexico, Oregon, South Dakota, Utah, and Wyoming (Fig. V).

Diagnosis and Discussion

This species is very similar to *I. pinta*. Males can be distinguished by the lighter pigment patterns of the head and pronotum, variable presence of crossveins in the radial sector of the forewings, narrower vesicle, less curved paraprocts, shape of spinulae pattern on 9th tergum, and spinulae pattern of the aedeagus. Females can be differentiated by the lighter pigment patterns of the head and pronotum, variable presence of crossveins in radial sector of the forewings, and longer, narrower subgenital plate. Nymphs can be separated by the lighter pigment patterns of the head and pronotum, presence of occipital ridge of spinulae, broadly rounded angles of the pronotum, and absence of a long dorsal hair at posterior margin of each cercal segment. Ova can be distinguished by the small, uniform chorionic punctations, lower chorionic ridges, and absence of highly elevated, ornate, multiple opening micropyles. The distribution of *I. phalerata* follows *I. pinta* closely except that it is not found as far North, and both species inhabit creeks and medium-size river systems (Fig. IV).

Authorship and type locality of this species have been confusing and incorrectly cited since its inception. The original description appeared in a paper by Smith (1917). She hesitantly placed it in *Dictogenus* and gave J. G. Needham authorship for the species, indicating that the description was quoted from his manuscript. Two specimens were mentioned in the text, one female from New Mexico which was designated as the holotype, and another female from Colorado (?/VI/1907, T. D. A. Cockerell). Needham and Claassen (1925) later reported that the specimen from Colorado was *Perla modesta*.

No life history or biological studies have been done. Based on the material examined, emergence begins in early May and continues until late Jul., with the largest numbers taken in mid-Jul.

Isoperla pinta Frison

Isoperla pinta Frison, 1937, 21:92. Holotype ♂; Floras Crk., Curry Co., Oregon, USA (INHS), allotype, Corvallis, Benton Co., Oregon, USA (INHS); (male head-pronotal pigment pattern, forewing, and genitalia; female subgenital plate; nymphal maxilla, labium, and habitus).

Isoperla tokula Hoppe, 1938, 4:157. Holotype ♂, and allotype

♀, Tokul Crk., Washington, USA (TBM); (male and female genitalia). Syn. Frison, 1942.

Isoperla pinta, Claassen, 1940, 232:204.

Isoperla pinta, Frison, 1942, 22:337. Syn. indicated.

Occiperla pinta, Banks, 1947, 54:280 (femur).

Isoperla pinta, Illies, 1966:416.

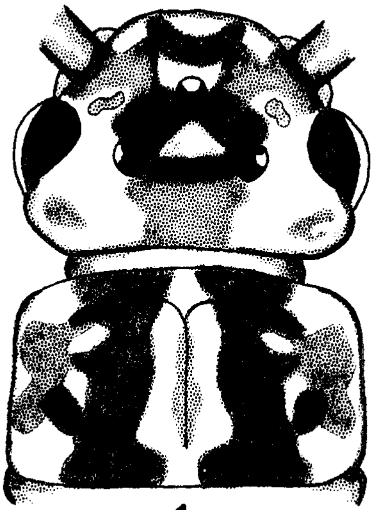
Isoperla pinta, Zwick, 1973:250.

Additional references: Isoperla pinta, Ricker, 1939 and 1943; Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Gaufin, 1964; Ricker, 1964; Knight et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia); Logan and Smith, 1966, Knight and Gaufin, 1966, 1967; Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Description (Plates VIII and IX)

Male (Pl. IX).-- Macropterous. Length of forewings 10-12 mm; length of body 9-11 mm. General body color medium brown. Head-pronotal pigment pattern with contrasting black, or dark brown and light yellow areas. Ocelli with dark brown pigment forming equalateral triangle; surrounded interocellar space light yellow; wide medium brown band extending from base of antennae to anterior ocellus; anterior frons with dark brown band (Fig. I). Pronotum with median yellow stripe, 2 wide, longitudinal black bands, and 2 mesolateral brown patches (Fig. I). Crossveins absent from

Plate IX, Figs. 1-8. *I. pinta*. 1. adult head and pronotum (scale: 1 mm = .05 mm). 2. male vesicle and 8th sternum (1 mm =.05 mm). 3. nymph head and pronotum (1 mm = .12 mm). 4. male terminalia, dorsal aspect (1 mm = .05 mm). 5. female subgenital plate (1 mm = .05 mm). 6. male paraproct, lateral aspect (1 mm = .01 mm). 7. male aedeagus, lateral aspect, A. large patch of small stout spinulae, B. large rounded anterior lobe, C. small mesoposterior lobe, D. scattered, long hair-like spinulae (1 mm = .03 mm). 8. female left forewing, A. radial sector (1 mm = .20 mm).



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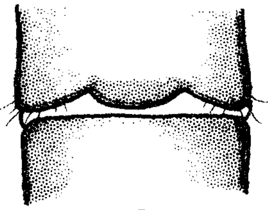

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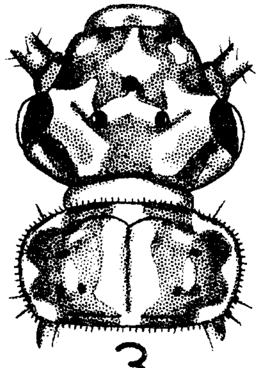

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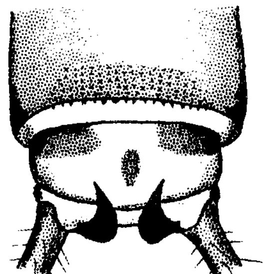

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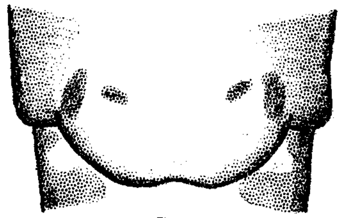

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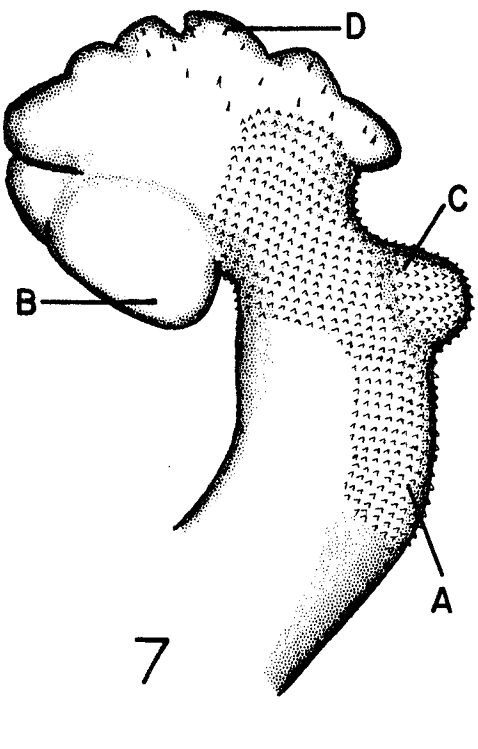

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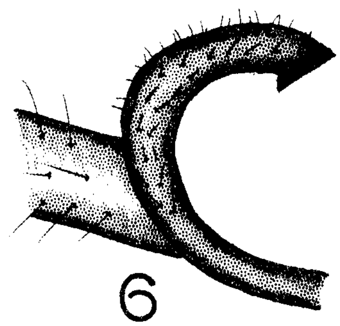

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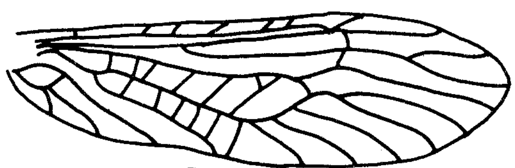

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radial sector of forewings (Fig. VIII). Ninth tergum with band of stout spinulae on posterior margin. Posterior 1/2, and median of 10th tergum light yellow, with dark brown mesal spot (Fig. IV). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts wide at base tapering apically to blunt tips with acute ventral spines that appear sharp from dorsal view; recurving anteriorly over 1/3 10th tergum, deflecting outward strongly; dorsal surface bearing small fine hairs (Figs. 4 & 6). Vesicle reduced, not projecting beyond anterior margin of 9th sternum; wider at base than apex, broadly rounded posteriorly and darker than rest of segment (Fig. II). Aedeagus entirely membranous, several small lobes at apex, one mesal posterolateral lobe void of spinulae (Fig. 7B), one mesoposterior lobe covered with small stout spinulae (Fig. 7C), apex with scattered long hair-like spinulae (Fig. 7D), large patch of concentrated small, stout spinulae covering posterior margin and mesal section (Fig. 7A).

Female (Pl. IX).-- Macropterous. Length of forewings 12-14 mm; length of body 10-12 mm. General body color, and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, produced 1/4 length of 9th sternum, rounded posteriorly with a shallow emargination (Fig. V).

Nymph (Pl. IX).-- Length of mature male nymph 11-13 mm;

length of mature female nymph 14-16 mm. Dorsum of head with median dark brown band extending from occiput to lateral ocelli, with narrow "Y"-arms extending antero-laterally behind lateral ocelli; anterior and lateral ocelli connected by 2 dark brown triangles, interocellar space light yellow, dark brown pigment pattern continuing to base of antennae and anterior margin of head, encircling 2 light yellow lateral spots on anterior frons; 2 heavy dark brown bands extending from occiput to back of compound eyes (Fig. III). Pronotum with median yellow stripe, contrasting patches of dark brown and yellow pigmentation; margin fringed with short setae, occasional long setae near corners; angles moderately rounded (Fig. III). Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal, and 8 rows of longitudinal stripes, 2 mesal, and 3 each laterally. Femora, tibiae, and tarsi with dorsal fringe of long fine hairs; dark brown band on femora before apex and on tibiae near proximad. Posterior margin of cercal segments with whorl of small, stout hairs; one long dorsal hair at posterior margin from 1st segment, one long ventral hair at posterior margin, and complete dorsal fringe of long hairs after 18th segment.

Ova (Pl. VIII).-- General shape oval, cross section circular (Fig. 1). Color light brown. Length .27 mm; width .19 mm. Collar well developed and expanded apically (Figs. 1 & 4). Chorion ornate with elevated, thickened ridges forming distinct hexagonal shaped depressions with smaller, largely unconnected ridges inside (Figs. 1, 2 & 3). Micropyles ornate, elevated with one to several openings, grouped 3 in a row near bottom 1/3, on one side (Figs. 2 & 3).

Material examined.-- TYPES: *I. pinta*, Holotype ♂, OREGON: Curry Co., Floras Crk., 20/V/1933, R. Dimick (INHS); allotype, OREGON: Benton Co., Corvallis, 5/V/1936, N. F. Larson (INHS). Paratypes; CANADA - BRITISH COLUMBIA: Cultus Lake, 24/IV/1935, W. E. Ricker, 1♀ (OSU[2]), Cultus Lake, 18/V/1933, W. E. Ricker, 1♂ (INHS), Cultus Lake, 13/V/1935, W. E. Ricker, 2♂, 3♀ (INHS), Cultus Lake, 24/IV/1935, W. E. Ricker, 2♂, 2♀ (INHS). USA - OREGON: Benton Co., Alsea, near Mill Crk., Alsea R., 22/V/1933, R. Dimick, 1♀ (INHS); Douglas Co., Winchester, N. Umpqua R., 22/III/1933, R. Dimick, 1♀ (INHS). Additional specimens - CANADA - BRITISH COLUMBIA: Cultus Lake, Sweltzer Crk., 2&4/VI/1937, W. E. Ricker, 71♂, 67♀ (WR), Cultus Lake, Sweltzer Crk., 8/IV/1937, W. E. Ricker, 27 nymphs (INHS), Cultus Lake, Sweltzer Crk., 13/III/1937, W. E. Ricker, 17 nymphs (WR), Cultus Lake, Sweltzer Crk., 26/IV/1937, W. E. Ricker, 2♂, 3♀ (WR), Cultus Lake, Reservoir Crk., 3&28/V/1935, W. E. Ricker, 1♂, 1♀ (INHS), Cultus Lake, Hatchery Crk., 16/V/1937, W. E. Ricker, 3♂, 6♀ (WR), Veder Crossing, 8/V/1937, W. E. Ricker, 1♀ (WR). USA - CALIFORNIA: Carmel Co., Locality ?, 23/V/1919, E. P. Van Duzee, 1♀ (CU); Lake Co., Anderson Springs, 30/IV/1955, R. Leuschner, 1♀ (WR); Merced Co., Merced R., 9/V/1937, P. W. C., 1♂, 1♀ (INHS); Santa Cruz Co., near Felton, 7/VI/1976, D. G. Denning, 1♀ (RWB); Trinity Co., Indian Crk. at mouth of Trinity R., 2/III/1955, S. G. Jewett, 1♂, 1♀ (UU). COLORADO: Grand Co., Parshall, Hwy. 40, Troublesome Crk., 13/VI/1964, Collector ?, 1♂ (UU), N. of Granby, Hwy. 40, Colorado R., 27/VI/1962, Collector ?, 1♀ (UU); Routt Co., 10 mi. E. of Craig, Yampa R., 18&20/VI/1968, B. R. Oblad, 2♂, 4♀ (UU), 1 mi. above Peterson's Ranch, Yampa R., 27/VI/1968, B. R. Oblad, 1♀ (UU), Steamboat Springs, Yampa R., 26/VI/1962, Collector ?, 1♂, 1♀ (UU), Steamboat Springs, Yampa R., 17/III/1968, B. R. Oblad, 2 nymphs (UU). IDAHO: Fremont Co., 5 mi. S. of Island Park, Hwy. 191, Snake R., 23/VI/1964, J. W. Richardson and S. L. Jensen, 3♀ (UU); Valley Co., 10 mi. S. of Cascades, Hwy. 15, Big Crk., 17/IV/1963, Collector ?, 1♂, 1♀ (RWB). MONTANA: Lewis and Clark Co., Arrastra Crk., 1/VII/1969, R. L. Newell, 1♀ (UU); Missoula Co., Buskhouse Bridge, Bitterroot R., 15/III/1969, B. R. Oblad, 1 nymph (UU); Teton Co., 2 mi. W. of Tetonia, Hwy. 33, Teton R., 22/VI/1964, J. W. Richardson and S. L. Jensen, 13♂, 20♀ (UU). OREGON: Benton Co., Philomath, Woods Crk., 24/IV/1936, W. M. Graf, 1♂ (INHS), Corvallis, 27/IV/1938, W. M. W., 2♂ (INHS); Clamath Co., 12 mi. E. of Chiloquin, Sprague R., 3/VII/1951, B. Malkin, 8♂, 9♀ (SJ); Clatsop Co., Youngs R., 1/V/1940, S. G. Jewett, 7♂, 24♀ (SJ), 4 mi. N.E. of Elsie, at Red Bluff, Nehalem R., 10/V/1965, S. G. Jewett, 1♂ (CU); Douglas Co., Cow Crk. at mouth of Quines R., 5/IV/1968, S. G. Jewett, 1♀ (RWB); Klamath Co., 12 mi. E. of Chiloquin, Sprague R., 1-3/VIII/1951, B. Malkin, 2♂, 1♀ (LCMNH); Lane Co., Indian Crk., 29/III/1940, S. G. Jewett, 2♂, 2♀ (UU). UTAH: Garfield Co., Asay Crk., 25/III/1959, A. R. Gaufin, 9 nymphs (UU); Peoa, Weber R., 19/II/1966, Collector ?, 1 nymph (UU); Ogden, Weber R., 25/V/1939, M. C. Tanner, 1 nymph (INHS). WYOMING: Carbon Co., Riverside, Madison R., 29/II/1964, Heaton, 6 nymphs (UU); Lincoln Co., Hwy. 189, La Barge Crk., 18/VII/1962, Collector ?, 1♀ (UU); Park Co., Yellowstone National Park, Norris Junct., 9/VI/1942, Collector ?, 1♂, 1♀ (RWB); Sublette Co., Daniel, Green R., 19/VII/1972, B. P. Stark, 1♂ (BS), N.W. of Daniel, Hwy. 187, Green R., 19/VII/1962, Collector ?, 1♂, 1♀ (RWB), Big Piney, Hwy. 189, S. Piney Crk., 18/VII/1962, Collector ?, 2♀ (UU).

Distribution.-- CANADA: British Columbia; USA: California, Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming (Fig. V).

Diagnosis and Discussion

I. pinta is closely allied with *I. phalerata* (see diagnosis and discussion under *I. phalerata*).

Knight and Gaufin (1966) reported that *I. pinta* was a stenothermic stonefly limited to altitudes below 8,500 feet. Knight and Gaufin (1967) found that *I. pinta* occurred in stony rivers, constant rivers, or sluggish rivers, and was associated most frequently with *Capnia limata* Frison, and *Utacapnia logana* (Nebeker and Gaufin) in the Gunnison River drainage system in Colorado.

No studies on the life history or general biology have been done. Based on the material examined, emergence begins in late Apr. along the Pacific Coast, and continues until mid-Jul. in the Central and Southern Rockies, with peak emergence occurring mid-Jun. This species inhabits creeks and medium-size rivers.

Species Group C

Isoperla sobria complex

This group is composed of *I.sobria* (Hagen), *I. gravitans* (Needham and Claassen), and a new species *I. tilasqua*. *I. sobria* (Hagen) is not included here since my study of the female and ova indicate that it is a synonym of *I. ebria*. These species all share the following characteristics: 1. large body size and dark pigment patterns; 2. male aedeagus entirely membranous, tubular, usually bearing one large patch or band of small, stout spinulae, and one or more patches of longer hair-like spinulae; 3. male vesicle usually reduced or obsolescent; 4. female subgenital plate truncate or broadly rounded, wide at base; and 5. ova with well-developed collar and chorion bearing evenly spaced small punctations; chorionic ridge development variable from slight to highly elevated.

The group is distributed from New Mexico, Colorado, Utah and Northern California, northward into Canada (Fig. VI). Species inhabit creeks and small- to medium-sized rivers. Emergence occurs from early Apr. until early Aug., and all are thought to undergo univoltine life cycles.

Isoperla sobria (Hagen)

Perla sobria Hagen, 1874, 7:577. Holotype ♀; Colorado mountains, Colorado, USA (MCZ #247).

Perla ebria, Hagen, 1874, 7:577. Holotype ♀; Colorado mountains, Colorado, USA (MCZ #248). NEW SYNONYMY.

Perlinella sobria, Banks, 1902, 34:123.

Isoperla ebria, Banks, 1907a:13.

Clioperla ebria, Needham and Claassen, 1925, 2:141 (male and female genitalia).

Clioperla sobria, Needham and Claassen, 1925, 2:143 (female genitalia).

Clioperla ebria, Claassen, 1940, 232:196.

Clioperla sobria, Claassen, 1940, 232:196.

Isoperla ebria, Ricker, 1943, 12:121 (adult and nymph head and pronotum, nymphal maxilla and habitus, and female genitalia).

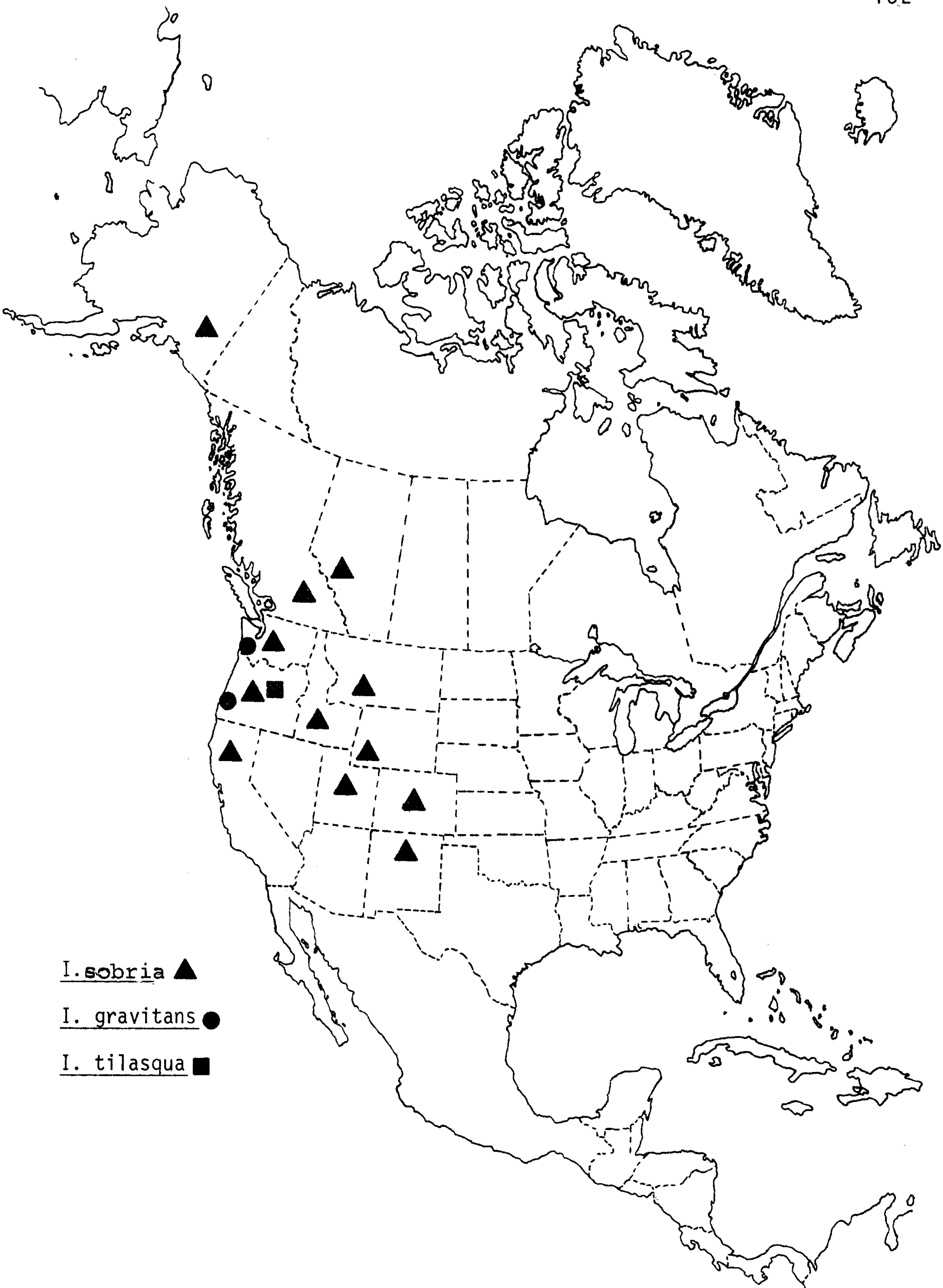
Isoperla ebria, Illies, 1966:401.

Isoperla sobria, Illies, 1966:420.

Isoperla ebria, Zwick, 1973:244.

Additional references: Isoperla ebria, Banks, 1907b; Dodds

Fig. VI. Distribution of the *I. sobria* complex


I. sobria ▲
I. gravitans ●
I. tilasqua ■

and Hisaw, 1929; Neave, 1929; Claassen, 1931 (description of nymph, no illustrations); Hoppe, 1938; Gaufin, 1955; Jewett, 1959 and 1960 (male and female genitalia); Knight et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia, and adult head and pronotum); Newell, 1970; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia, and adult head and pronotum); Stewart et al., 1974; Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia and adult head and pronotum). Isoperla sobria, Banks, 1907a.

Description (Plates X and XI)

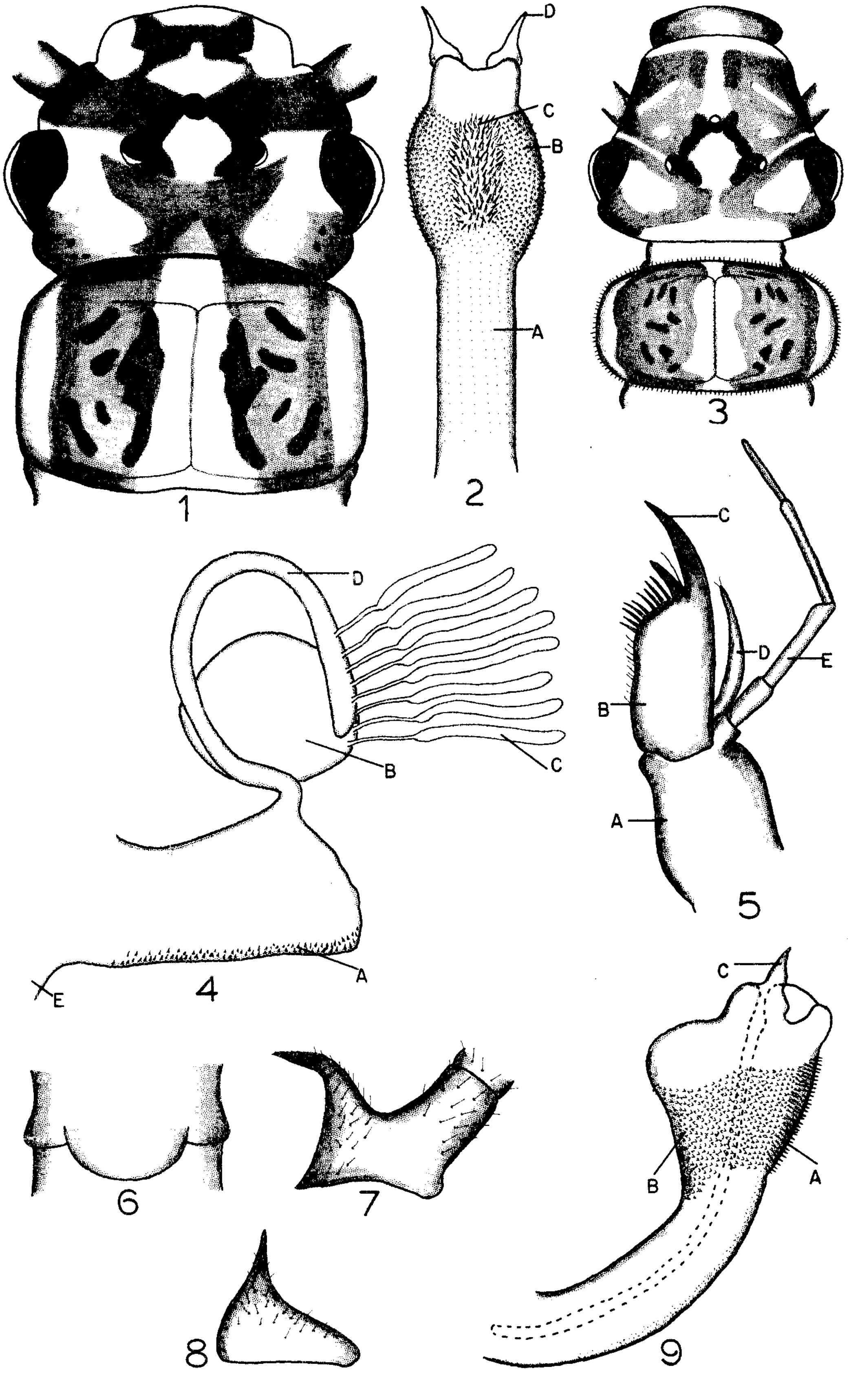
Male (Pl. X).-- Macropterous. Length of forewings 9-11 mm; length of body 8-11 mm. General body color medium to dark brown. Head-pronotal pigment pattern dark. Ocelli connected by triangular dark pigment, extending outward from anterior ocellus to antennal bases; wide bowl-shaped medium brown pigment band on back of head to lateral ocelli; interocellar space light; anterior frons with dark transverse band, connected posteriorly with ocellar-antennal band and enclosing triangular light spot; posterolateral margins of head with medium brown pigment and dark spots (Fig. 1). Pronotum with median yellow stripe, and dark brown rugosities (Fig. I). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of cercal segments with long ventral hair.

Paraprocts very broad at base, tapering apically to acute, fine tips covered with small, fine hairs, and recurving slightly over 10th tergum (Figs. 7 & 8). Vesicle obsolescent. Aedeagus entirely membranous, tubular, apically expanded; expanded portion bearing transverse wide band of small, stout spinulae (Figs. 2B & 9B), interrupted at posterior margin by narrow vertical band of long hair-like spinulae (Figs. 2C & 9A); apex void of spinulae with 2 pointed lobes (Figs. 2D & 9C); proximal stalk covered with very small, dispersed spinulae (Fig. 2A).

Female (Pl. X).-- Macropterous. Length of forewings 11-13 mm; length of body 10-13 mm. General body color, and head-pronotal pigment pattern similar to male. Subgenital plate broad at base, produced posteriorly 1/4 length of 9th sternum, often broadly rounded posteriorly (Fig. 6) (sometimes truncate with shallow, median emargination). Vagina with narrow ventral band of small stout spinulae (Fig. 4A), and seminal receptacle (Fig. 7B) with 8 accessory receptacular glands (Fig. 7C).

Nymph (Reared) (Pl. X).-- Length of mature male nymph 10-11 mm; length of mature female nymph 12-14 mm. Dorsum of head with diamond-shaped narrow dark band, open at back, connecting ocelli; 2 circular lighter brown pigment bands enclosing light spots behind eyes; frons mostly brown except T-shaped light area and pair each of enclosed light bands and spots (Fig. 3). Laciniae with 2 large

Plate X, Figs. 1-9. I. sobria. 1. adult head and pronotum (scale: 1 mm = .05 mm). 2. male aedeagus, posterior aspect, A. proximal tube with very small scattered spinulae, B. transverse, wide band of concentrated small stout spinulae, C. mesoposterior band of long hair-like spinulae, D. apical pointed lobe (1 mm = .04 mm). 3. nymph head and pronotum (1 mm = .08 mm). 4. female vagina, A. vaginal armature, B. seminal receptacle, C. receptacular duct, D. accessory receptacular glands, E. subgenital plate (1 mm = .02 mm). 5. nymphal maxilla, A. stipe, B. lacinia, C. apical tooth, D. galea, E. maxillary palpus (1 mm = .04 mm). 6. female subgenital plate (1 mm = .09 mm). 7. male paraproct, lateral aspect (1 mm = .02 mm). 8. male paraproct, dorsal aspect (1 mm - .02 mm). 9. male aedeagus, lateral aspect, A. mesal posterior band of long hair-like spinulae, B. transverse, wide band of concentrated small stout spinulae, C. apical pointed lobe (1 mm = .04 mm).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teeth; subapical tooth approximately 1/2 length of apical tooth, inner lacinial margin with row of 8-10 long stout hairs, row of irregular slender hairs below long stout hairs (Fig. 5). Pronotum with median yellow stripe, 2 wide longitudinal suffused brown bands with dark rugosities, and fringed with small setae (Fig. 3). Abdominal terga with paired longitudinal rows of light areas lateral to median, and 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Femora with scattered dorsal fringe of long fine hairs, tibiae with continuous dorsal fringe, and tarsi with few long dorsal hairs. Posterior margin of cercal segments with whorl of small, stout hairs, one long dorsal and ventral hair at posterior margin after 18th segment, continuous dorsal and ventral fringe after 21st segment.

Ova (Pl. XI).-- General shape oval, cross section circular (Fig. I). Color medium brown. Length .29 mm; width .22 mm; collar well developed and expanded at apex, base with a depression void of chorionic sculpturing (Figs. 1, 2 & 4). Chorion evenly spaced small punctations, ridges barely evident (Figs. 1, 2 & 3). Micropyles undetected.

Material examined.-- TYPES: *I. ebria*, Holotype ♀, USA - COLORADO: Colorado mountains, 1873, Collector ? (MCZ #248). *I. sobria*, Holotype ♀, USA - COLORADO: Colorado mountains, 1873, Collector ? (MCZ #247). Additional specimens - CANADA - ALBERTA: Maligne Lake, 21/VII/1925,

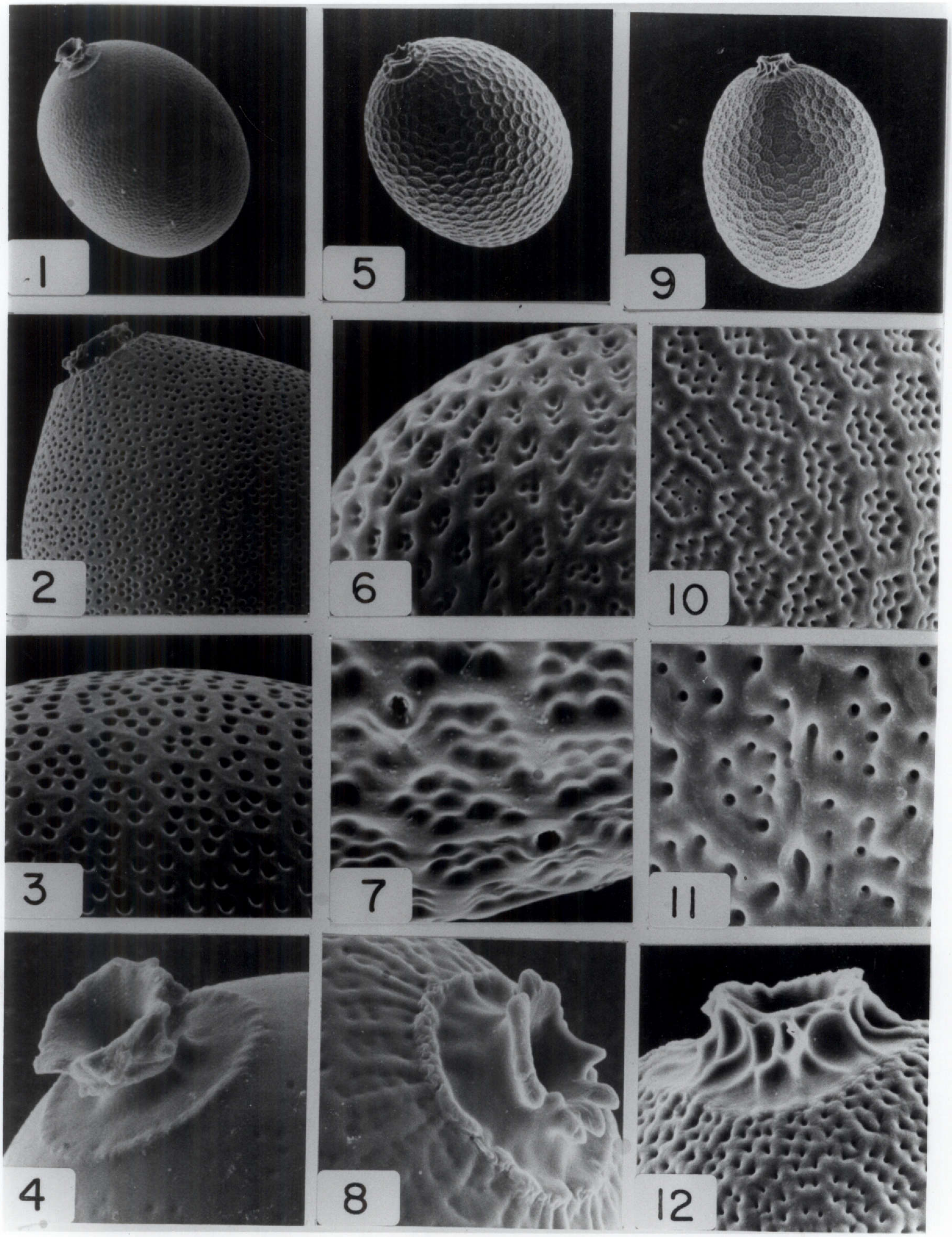
Plate XI. Scanning electron micrographs of *Isoperla* ova.*

Figs. 1-4. *I. sobria*. 1. whole ova 200X. 2. detail anterior 1/2 400X. 3. detail of chorion 1000X. 4. detail of collar 1000X.

Figs. 5-8. *I. gravitans*. 5. whole ova 200X. 6. detail of chorion 700X. 7. detail of micropyles 200X. 8. detail of collar 1000X.

Figs. 9-12. *I. tilasqua*. 9. whole ova 200X. 10. detail of chorion 1000X. 11. detail of micropyles 2000X. 12. detail of collar 1000X.

* magnifications represent original values before reduction of plates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F. Neave, 2♀ (INHS), Maligne Lake, 2/VII/1915, Collector ?, 1♂, 5♀ (CU), Banff, 18/VI/1925, O. Bryant, 1♂ (CU), Lake Louise, 4/VIII/1927, C. R. Crosby, 1♀ (CU). BRITISH COLUMBIA: Penticton, Shingle Crk., 19/IV/1935, A. N. G., 1 nymph (INHS), Penticton, Shingle Crk., 13/V/1935, A. N. G., 1♂, 1 exuvia (INHS). USA - CALIFORNIA: Nevada Co., Spring Trib. to Sagehen Crk., 11-12 & 31/VIII/1965, A. L. Sheldon, 4♂, 7♀, 16 nymphs (USNM), Sagehen Crk., 30/V/1966, A. L. Sheldon, 1♀ (USNM), Sagehen Crk., 13/IX/1965, A. L. Sheldon, 4♂, 1♀ (USNM); Siskiyou Co., Shasta, head of Sacremento Mt., 5/VI/1965, S. G. Jewett, 1♂, 2♀ (CU); Tuolumne Co., Yosemite National Park, Date ?, H. J. Raynor, 1♂, 2♀ (CU). COLORADO: Grand Co., Rocky Mt. National Park, Chasm Falls, 27/VII/1938, J. A. and H. H. Ross, 1♂, 2♀ (INHS), Rocky Mt. National Park, Fall R., 24/VII/1960, A. R. Gaufin, 1♀ (UU); Routt Co., Green Crk., 16/VII/1968, B. R. Oblad, 1♀ (UU); County ?, Independence Pass, Lake Crk., 6/VIII/1943, J. A. and H. H. Ross, 2♀ (INHS), Clairsden, Trib. of Smith Crk., 11/VI/1952, W. E. Ricker, 2♂, 3♀ (WR). MONTANA: Gallatin Co., Locality ?, 15/VII/1913, Collector ?, 1♀ (CU), Hyalite Crk., 13/VI/1951, R. Hays, 1♂, 3 exuviae (UU); Glacier Co., Glacier National Park, below Red Rock Lake, Swift Current Crk., 18/VII/1966, A. R. Gaufin, 1♀ (RWB), Trib. of Wilber Crk., 19/VII/1966, J. L. Miner, 1♀ (RWB), Many Glacier Area, Lake Josephine, 9/VIII/1966, A. R. Gaufin, 1♀ (RWB), Glacier National Park, Many Glacier Area, Lower Area D, 21/VIII/1966,

A. R. Gaufin, 1♀ (UU), Glacier National Park, Elizabeth Crk., 10/VII/1970, C. M. Yarmoloy, 1♂, 1♀ (UU); Park Co., 1/2 mi. above Hwy. 212, Island Lake, 28/VII/1966, J. R. Grierson, 1♂ (UU), above W. Fork of Bitterroot R., Trapper Crk., 30/VI/1965, J. R. Grierson, 1♂ (UU), S. of Darby, Hwy. 93, Fern Crk., 18/VI/1965, A. R. Gaufin, 1♀ (UU). NEW MEXICO: Santa Fe Co., Big Tesuque Campground, Big Tesuque Crk., 10/VI/1974, B. P. Stark and T. A. Wolff, 1♂ (BS); Taos Co., Rio Trampos, 20/IV/1973, B. P. Stark and T. A. Wolff, 1 nymph (BS). OREGON: Benton Co., Muddy Crk., 12/IV/1938, S. G. Jewett, 4 nymphs (SGJ); Clackamas Co., Mollala R., 13/VI/1938, S. G. Jewett, 1♀ (INHS); Deschutes Co., Fall R., 13/VII/1948, S. G. Jewett, 4♂, 17♀ (UU), Fall R., 7/VI/1949, S. G. Jewett, 1 nymph (SGJ); Hood R. Co., Hood R. Meadows, 10/VIII/1955, S. G. Jewett, 1♂, 1♀ (UU); Klamath Co., Crater National Park, Annie Crk., 24/VI/1956, J. Schuh, 2♂, 2♀ (OSU[2]), Collier State Park, 21/IV/1951, S. G. Jewett, 11♂, 18♀ (UU), Cherry Crk., 26/VI/1937, S. G. Jewett, 1♀ (INHS), Upper Klamath R., Denny Crk., 19/V/1952, S. G. Jewett, 4♂, 3♀ (SGJ). UTAH: Salt Lake Co., Brighton, Big Cottonwood Crk., 6/IV/1954, A. R. Gaufin, 4♀, 35 nymphs (UU), Brighton, Big Cottonwood Crk., 15/V/1954, A. R. Gaufin, 17 nymphs (UU), Lambs Canyon Crk., 26/V/1965, R. W. Baumann, 6 nymphs (RWB), Pinecrest, Emigration Canyon, 26/IX/1966, R. W. Baumann, 4 nymphs (RWB);

Uintah Co., Roosevelt, Cottonwood Crk., 15/VI/1936, F. C. Harmston, 2♂ (INHS); Wasatch Co., Trout Crk., 30/VI/1965, D. C. Hales, 1♂ (UU), Trout Crk., 18/III/1966, D. C. Hales, 1 nymph (UU). WYOMING: Albany Co., Centennial, 2/VII/1938, D. J. and J. N. Knull, 1♂ (INHS), Gold Nesh Fork Crk., 23/VII/1972, W. E. Ricker, 1♀, 1 nymph (SGJ), Foxpark, 4/VII/1938, Collector ?, 2♀ (UU); Park Co., above Hwy. 212, Beartooth Crk., 28/VII/1966, J. R. Grierson, 1♂ (RWB), 7 mi. E. of Mammoth Hot Springs, Blacktail Deer Crk., 26/VI/1964, J. W. Richardson and S. L. Jensen, 1♂ (RWB).

Distribution.-- CANADA: Alberta, British Columbia; USA: Alaska, Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, and Wyoming (Fig. VI).

Diagnosis and Discussion

I. sobria is most similar to *I. tilasqua*. Males can be distinguished by the absence of a vesicle on the 8th sternum, longer, thinner, more acute paraprocts, aedeagus bearing only one posterior patch of long, hair-like spinulae, 2 pointed dorsal lobes, apex void of spinulae, and narrower patch of small stout spinulae. Females can be differentiated by the broadly rounded subgenital plate void of small hairs. The nymph of *I. tilasqua* is unknown. Ova can be distinguished from those of *I. tilasqua* by the lower chorionic ridges, and depressed area void of sculpturing at base of the collar.

I. ebria (Hagen) is placed in synonymy with *I. sobria* (Hagen) based on a direct comparison of the type specimens and scanning electron microscope study of the ova. The type specimen of *I. ebria* exhibited a broadly rounded subgenital plate but in the type of *I. sobria* there was a median emargination. This variation was noted in many of the *I. sobria* populations examined. The ova from both types were identical, and no variation in aedeagal characters was observed over the geographic range of *I. sobria*.

Dodds and Hisaw (1925) reported that *I. ebria* was distributed between 5,500-11,000 feet in the Colorado Rockies. No studies on the life history or general biology have been done. Material examined indicated emergence occurs in mid-May to early Aug., with largest numbers collected early-Jul. Nymphs are found in creeks and small- to medium-sized rivers.

Isoperla gravitans (Needham and Claassen)

Clioperla gravitans, Needham and Claassen, 1925, 2:138.

Holotype ♂: Olympia, Thurston Co., Washington, USA, (CU-Type is missing), (wings and male genitalia).

Isoperla gravitans, Hoppe, 1938, 4:156.

Clioperla gravitans, Claassen, 1940, 232:196.

Isoperla gravitans, Jewett, 1954, 11:548. Allotype ♀: Youngs R., Clatsop Co., Oregon, USA, 1/V/1940, S. G. Jewett (CAS), (female genitalia).

Isoperla gravitans, Illies, 1960:405.

Additional references: Isoperla gravitans, Jewett, 1959, (male and female genitalia).

Description (Plate XI and XII)

Male (Pl. XII).-- Macropterous. Length of forewings 14-16 mm; length of body 12-15 mm. General body color medium brown. Head pattern consisting of dark "H"-shaped mark in center, and lighter brown transverse bar across frons between eyes (Fig. I). Pronotum with median yellow stripe; discs with wide longitudinal medium brown pigment band and vermiculate markings (Fig. I). Forewings light, veins dark brown. Femora, tibiae and tarsi dark brown; femora with light yellow band at distal end. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Cerci dark brown, bearing small fine hairs. Paraprocts short, stout, tapering to blunt points apically, broad at base, appearing triangular from above, recurving anteriorly barely over 10th tergum, and bearing medium fine hairs (Fig. 3 & 4). Vesicle, very broad at base, rounded at apex, much lighter than rest of segment (Fig. 2). Ninth sternum and tergum much lighter than rest of abdominal segments. Aedeagus entirely membranous, tubular, apex expanded into large rounded lobe void of spinulae; small nipple at anterodorsal margin, large posteromesal lobe with "T"-shaped band of medium length spinulae and 2 spinulae free patches posteriorly (Figs. 5B & 6D); band of scattered fine spinulae encircling mesal section, interrupted before posteromesal lobe (Figs. 5D & 6C), wide band of small stout spinulae encircling aedeagus below posteromesal lobe (Figs. 5C & 6B), small patch of medium-length stout spinulae at posteroventral margin (Figs. 5A & 6A).

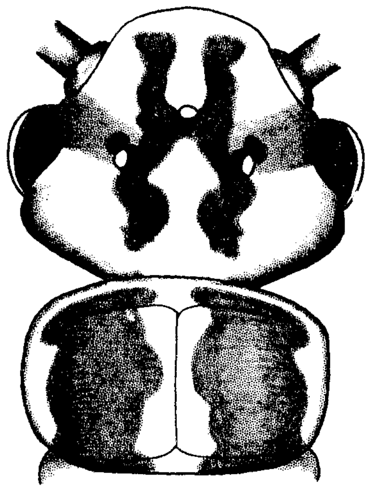
Female (Pl. XII).-- Macropterous. Length of forewings 16-20 mm; length of body 15-18 mm. General body color and head-pronotal pigment pattern similar to male. Subgenital plate truncate, lateral margins parallel with sides of abdomen, shallow median emargination at posterior margin; produced 2/3 length over 9th sternum; 2 sclerotized patches on inner surface at posterolateral margins, lighter than rest of segment; light pigmentation extending to base of 8th sternum forming "V"-shaped pattern (Fig. 7). Ninth and 10th abdominal segments lighter than rest.

Nymph.-- Unknown.

Ova (Pl. XI).-- General shape oval, cross section circular (Fig. 5), color medium brown. Length .30 mm; width .24 mm. Collar well developed and expanded apically (Figs. 5 & 8). Chorionic ridges elevated forming distinct hexagonal depressions bearing 4-7 evenly spaced punctations (Figs. 5-7). Micropyles arranged in pairs on top of ridges near bottom 1/3 on one side (Fig. 7).

Material examined.-- USA - OREGON: Benton Co., Oak

Plate XII, Figs. 1-7. _I. gravitans_. 1. adult head and pronotum (scale: 1 mm = .08 mm). 2. male vesicle and 8th stern-m (1 mm = .07 mm). 3. male paraproct, lateral aspect (1 mm = .02 mm). 4. male paraproct, dorsal aspect (1 mm = .02 mm). 5. male aedeagus, lateral aspect, A. posteroventral patch of medium-length stout spinulae, B. posteromesal lobe with "F"-shaped band of medium length spinulae, C. wide band of small stout spinulae, D. mesal band of scattered fine spinulae (1 mm = .04 mm). 6. male aedeagus, posterior aspect, A. posteroventral patch of medium-length stout spinulae, B. wide band of small stout spinulae, C. mesal band of scattered fine spinulae, D. posteromesal lobe with "T"-shaped stout spinulae (1 mm = .04 mm). 7. female subgenital plate (1 mm = .03 mm).



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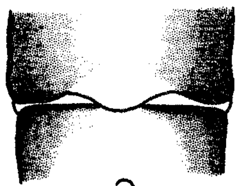

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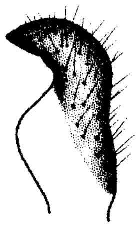

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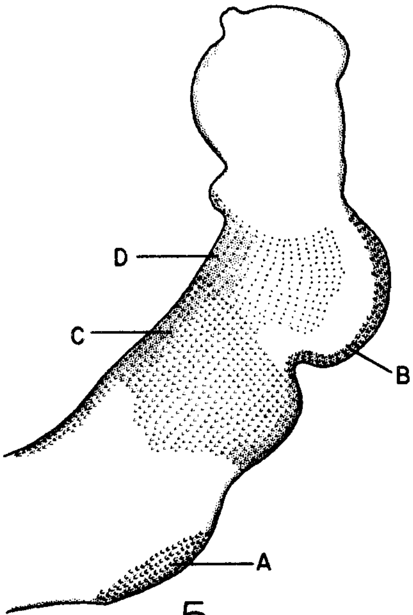

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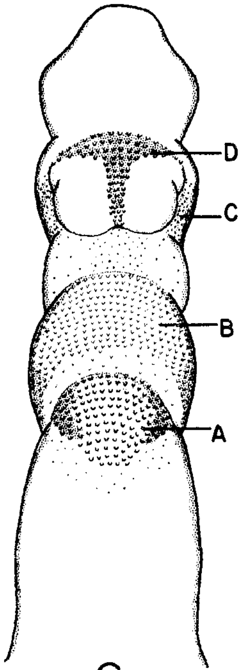

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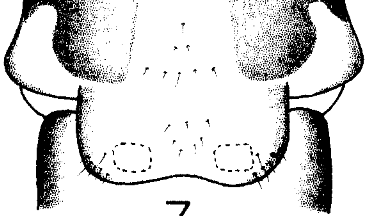

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Crk., 17&19/V/1968, C. D. Kerst, 1♂, 5♀ (RWB), Oak Crk., 18/IV/1935, R. Dimick, 2♀ (WR), Oak Crk., 16/V/1969, C. D. Kerst, 1♂ (USNM), Oak Crk., 10/V/1969, C. D. Kerst, 1♂, 1♀ (SJ), Oak Crk., 7/V/1969, C. D. Kerst, 1♂, 3♀ (USNM); Clackamas Co., Mt. Hood, Still Crk. Campground, 17/VI/1967, S. W. Jewett, 2♀ (USNM); Clatsop Co., 2 mi. E. of Elsie, Osweg Crk., 3/V/1964, S. G. Jewett, 1♂ (SJ), 4 mi. N.E. of Elsie, at Red Bluff, Nehalem R., 10&11/V/1965, S. G. Jewett, 1♂, 2♀ (RWB); Columbia Co., Clatskanie, Beaver R., 9/V/1936, J. Schuh, 1♂, 4♀ (WR). WASHINGTON: Clark Co., Ellsworth, 14/VI/1941, S. G. Jewett, 2♂ (SJ), Ellsworth, 27/III/1941, S. G. Jewett, 1♀ (SJ), Ellsworth, 1/IV/1941, S. G. Jewett, 1♂ (WR); King Co., Fall City, Raging R., 30/IV/1932, G. N. Hoppe, 1♂ (WR).

Distribution.-- USA: Oregon and Washington (Fig. VI).

Diagnosis and Discussion

I. gravitans is most similar to *I. tilasqua*. Males can be distinguished by the wide, longitudinal, medium brown bands on pronotum, light yellow vesicle, light yellow 9th and 10th abdominal segments, stouter paraprocts, absence of 2 long narrow apical lobes, and 2 posterior patches of long hair-like spinulae on aedeagus. Females can be separated by the pigment patterns mentioned above, lighter pigmentation of the subgenital plate, presence of 2 sclerotized patches on inner surface at posterolateral margins, and light 9th and 10th abdominal segments. Ova can be differentiated by the thicker chorionic ridges, larger size, fewer punctations in each depression, and the absence of a small groove preceding each micropyle opening.

Needham and Claassen (1925) described this species from a single male specimen, and indicated that it was in the Cornell University collection, although Cornell has no record of it ever being received or deposited.

No life history or general biology data are available for this species. Based on the material examined, emergence occurs early Apr. to mid-Jun., with largest numbers collected mid-May. Nymphs are found in creeks and small rivers.

Isoperla tilasqua NEW SPECIES

Description

Male (Pl. XII).-- Macropterous. Length of forewings 10-12 mm; length of body 11-12 mm. General body color dark brown. Head-pigment pattern dark. Lateral ocelli connected to anterior ocellus by a dark brown inverted "U"-shaped band; interocellar space light; arms of the inverted "U"-band connected to back margin of head by progressively diminishing vermiform brown pigmentation; 2 large ovate dark brown spots connecting anterior ocellus to base of antennae; pair of club-shaped marks extending from these spots onto anterior frons (Fig. I). Pronotum mostly light brown, with median light stripe, dark brown lateral rugosities and anterior transverse dark band (Fig. I). Abdominal terga with 8 rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of each cercal segment with long ventral hair. Paraprocts short, stout, tapering to points apically, bearing small fine hairs, and recurving forward to level of 10th tergum (Fig. 3). Vesicle, broad at base, rounded at apex, and darker than rest of segment (Fig. 2). Aedeagus entirely membranous, tubular and constricted near middle; 2 long narrow tubular lobes apically (Fig. 5F); one posteroventral lobe bearing long hair-like spinulae patch which extends into a longitudinal band (Figs. 4 & 5A); constricted section bearing concentrated patch of small, fine spinulae (Figs. 4 & 5C), (Pl. VI, Figs. 9 & 10), and narrow posterior band of long hair-like spinulae bifurcated at apex (Figs. 4 & 5D), (Pl. VI, Fig. 10); dorsum expanded bearing scattered small fine spinulae (Figs. 4 & 5D); proximal 1/2 bearing small stout spinulae (Figs. 4 & 5B), (Pl. VI, Fig, 8).

Female (Pl. XII).-- Macropterous. Length of forewings 13-16 mm; length of body 15-17 mm. General body color, and head-pronotal pigment pattern similar to male. Subgenital plate truncate, lateral margins parallel with sides of abdomen, produced posteriorly 1/4 length of 9th sternum, bearing scattered fine hairs (Fig. 6).

Nymph.-- Unknown.

Ova (Pl. XI).-- General shape oval, cross section circular (Fig. 9). Color light brown. Length .28 mm; width .21 mm. Collar well developed with outer partitioned projections (Figs. 9 & 12). Chorionic ridges raised forming distinct hexagonal depressions with 8-14 evenly spaced small punctations (Figs. 9-12). Micropyles with a small groove preceding each opening, and arranged in pairs on top of ridges near bottom 1/2 on one side (Fig. 2).

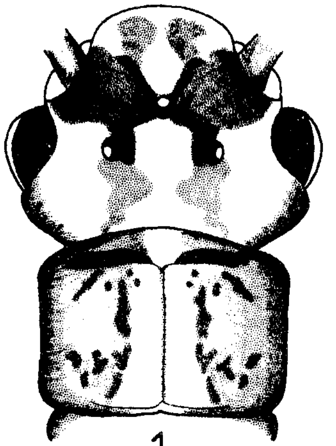
Material examined.-- TYPES: Holotype ♂, USA - OREGON: Benton Co., Trap 1, Oak Crk., 13/VI/1968, C. D. Kerst (USNM); allotype ♀, USA - OREGON: Benton Co., Trap 2, Oak Crk., 22/V/1969, C. D. Kerst (USNM). Paratypes, OREGON: Benton Co., Trap 2, Oak Crk., 19-22/VI/1968, C. D. Kerst, 1♀ (USNM), Trap 1, Oak Crk., 16-18/V/1969, C. D. Kerst, 1♂ (USNM); Clackamas Co., Mt. Hood, Still Crk. Campground, 17/VI/1967, S. G. Jewett, 2♀ (USNM); Clatsop Co., Big Crk., 9/V/1947, S. G. Jewett, 1♂ (SGJ); Columbia Co., Keasy, Rock Crk., 23/V/1954, S. G. Jewett, 1♀ (SGJ); Klamath Co., Spring Crk., 8/V/1967, J. Schuh, 2♀ (USNM); Lane Co., Fern Ridge Res., 1/V/1946, S. G. Jewett, 1♀ (SGJ), (Paratypes deposited at USNM, SJ, SWS & NTSU).

Distribution.-- USA: Oregon (Fig. VI).

Diagnosis and Discussion

I. tilasqua is most closely allied with *I. ebria* based on male and female genital characters and pigment patterns (see diagnosis under *I. ebria*). Ova are more similar to

Plate XIII, Figs. 1-6. *I. tilasqua*. 1. adult head and pronotum (scale: 1 mm = .08 mm). 2. male vesicle and 8th sternum (1 mm = .08 mm). 3. male paraproct, lateral aspect (1 mm = .03 mm). 4. male aedeagus, posterior aspect, A. posteroventral lobe bearing patch bearing long hair-like spinulae, B. wide band of small stout spinulae, C. constricted section bearing concentrated small stout spinulae, D. narrow posterior band of long, hair-like spinulae, E. expanded apex with scattered small fine spinulae (1 mm = .05 mm). 5. male aedeagus, lateral aspect, A. posteroventral band of long hair-like spinulae, B. wide band of small stout spinulae, C. constricted section bearing concentrated small stout spinulae, D. narrow posterior band of long, hair-like spinulae, E. expanded apex with scattered small fine spinulae, F. dorsal tubular processes (1 mm = .04 mm). 6. female subgenital plate (1 mm = .02 mm).



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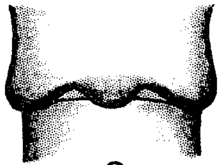

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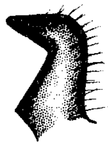

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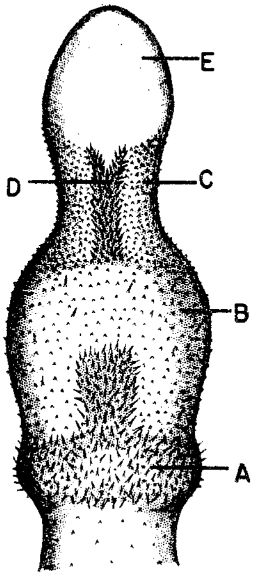

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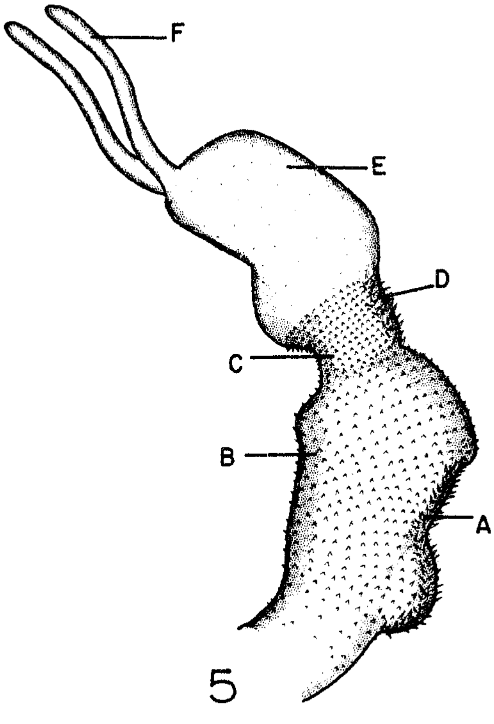

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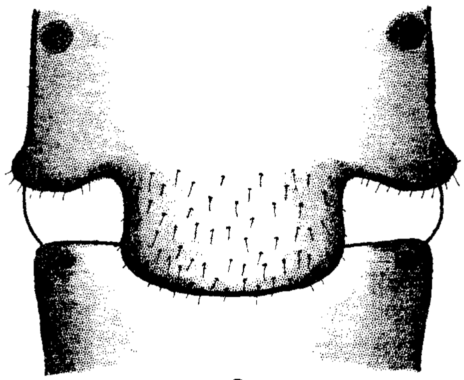

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I. gravitans, having well-developed chorionic ridges and distinct hexagonal-shaped depressions with many evenly spaced punctations.

This species is found in small- to medium-sized creeks and is limited to the Coastal and Cascade Mountain Ranges in Oregon (Fig. VI). Emergence begins in early May and continues until mid-Jun.

Etymology.-- The name "tilasqua" was taken from the Indian name for big creek. The first specimen of this species examined was from Big Creek, in Clatsop County, Oregon.

Species Group D

Isoperla marmorata complex

This group is composed of *I. fulva* Claassen and *I.* marmorata (Needham and Claassen). They share the following characteristics: 1. male aedeagus bearing a spinose, club-shaped, sclerotized process; 2. broadly rounded, shallow male vesicle; 3. broad variable-shaped subgenital plate, often angulate; 4. nymphal head pattern with interocellar space, frons and clypeus mostly dark brown; 5. two wide longitudinal concolorous dark brown bands with no rugosities on nymphal pronotum; 6. dorsal fringe of long fine hairs on nymphal tibiae and tarsi; 7. 2 wide dark brown lateral stripes and one narrow median light brown stripe on nymphal abdominal terga; and 8. ova with developed collar and elevated thickened chorionic ridges forming distinct hexagonal depressions with evenly spaced small punctations.

I. marmorata is mainly restricted to the Coastal, Cascade, and Olympic mountain ranges along the Pacific Coast, and occurs in small creeks to medium-sized rivers. *I. fulva* has a broad distribution from the Southern, Central and Northern Rocky Mountains to the Pacific Coast (Fig. VII), and inhabit creeks and rivers of all sizes. Emergence occurs from early May in southern latitudes until Aug. in the north; both species are thought to undergo univoltine life cycles.

Isoperla marmorata (Needham and Claassen)

Clioperla marmorata, Needham and Claassen, 1925, 2:142. Holotype ♀; Reno, Washoe Co., Nevada, USA (CU #1,166), (wings and female genitalia).

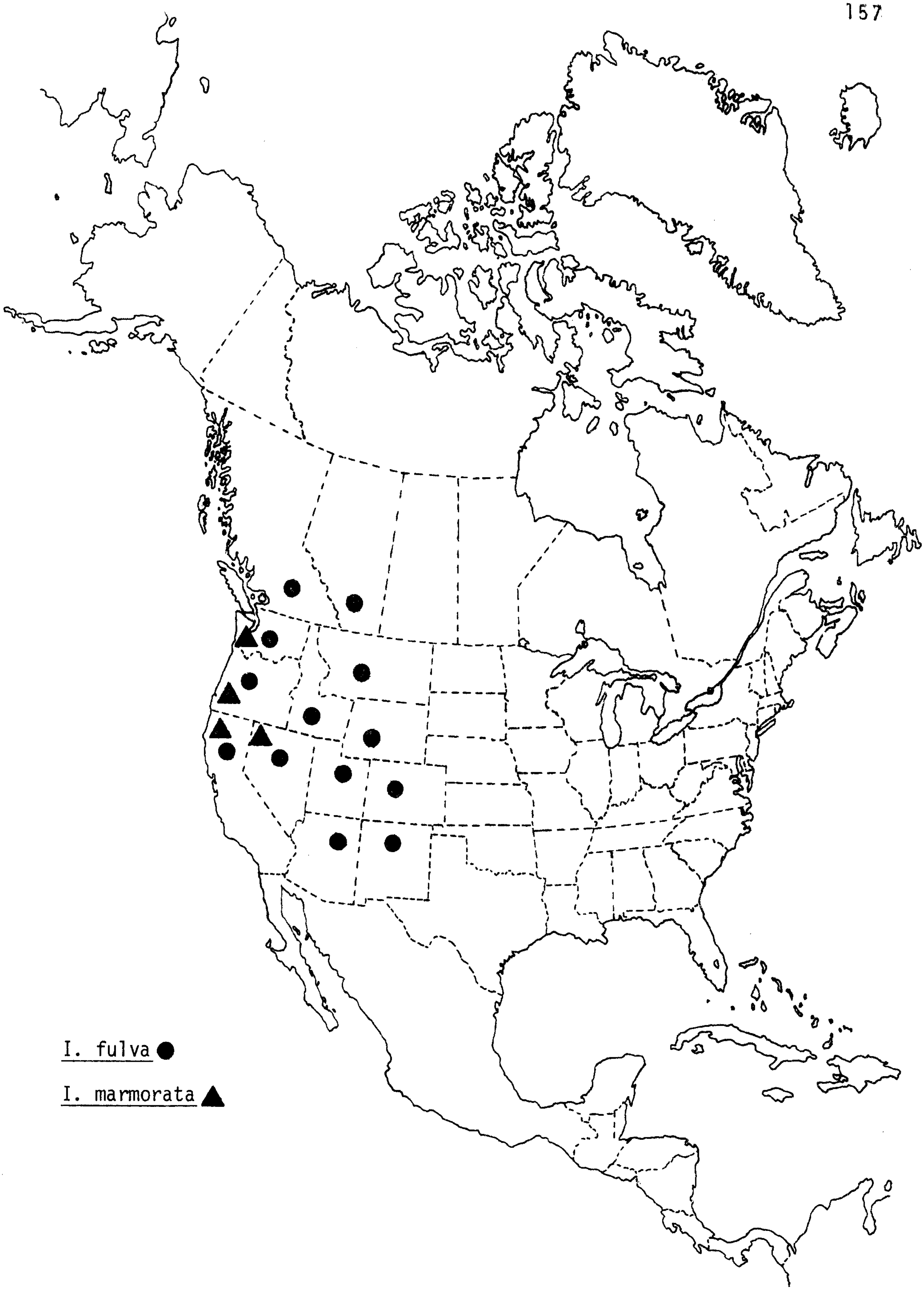
Clioperla marmorata, Claassen, 1940, 232:196.

Isoperla marmorata, Jewett, 1954b, 30:178. Allotype ♂; Eagle Crk., Clackamas Co., Oregon, USA (CAS), (male genitalia).

Isoperla marmorata, Illies, 1966:409.

Additional references: *Isoperla marmorata*, Jewett, 1956, 1959 and 1960 (wings and male genitalia); Sheldon and Jewett, 1967; Kerst and Anderson, 1974 and 1975.

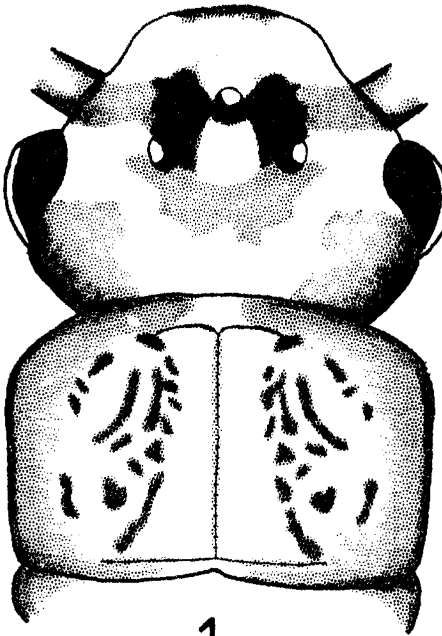
Fig. VII. Distribution of the *I. marmorata* complex


I. fulva
I. marmorata

Description (Plates XIV and XV)

Male (Pl. XIV).-- Macropterous. Length of forewings 9-11 mm; length of body 9-11 mm. General body color medium brown. Ocelli of head connected by distinct dark brown "M"-shaped pigment pattern; interocellar space light yellow; light brown pigment band extending across top "M"-band between antennal bases; wide median light brown band on anterior frons, and light brown, variable patch of pigmentation connecting lateral ocelli; large brown patch behind each eye (Fig. 1). Pronotum light brown with median yellow stripe and small vermiform dark brown rugosities (Fig. I). Wings hyaline, veins light brown, anal area of hind wings fumose. Femora, tibiae, and tarsi medium brown, femora with yellow band at distal end. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts wide at base, tapering to long fine points apically, bearing scattered small fine hairs (Fig. 4). Cerci with one long ventral hair at posterior margin; anterior 1/4 of each segment lighter than remainder. Vesicle shallow, broadly rounded, darker than rest of segment (Fig. 3). Aedeagus capitate; expanded apex bearing scattered, large rounded spinulae (Fig. 5F) and median nipple void of spinulae (Fig. 5G); posterior margin with thin sclerotized process appearing clavate laterally and bearing a row of small spines dorsally and ventrally on expanded portion (Fig. 5D); patch of large stout spines above insertion of

Plate XIV, Figs. 1-6. _I. marmorata_. 1. adult head and pronotum (scale: 1 mm = .03 mm). 2. nymph head and pronotum (1 mm = .03 mm). 3. male vesicle and 8th sternum (1 mm = .05 mm). 4. male paraproct, lateral aspect (1 mm = .01 mm). 5. male aedeagus, lateral aspect, A. proximal stalk bearing scattered, small, fine, hair-like spinulae, B. expanded basal lobe bearing scattered small spinulae, C. small mesoposterior nipple-like lobe, D. sclerotized process, E. patch of large stout spines, F. expanded apex bearing scattered, large rounded spinulae, G. mesodorsal nipple, H. mesal band of dense small, stout spinulae (1 mm = .03 mm). 6. female subgenital plate (1 mm = .06 mm).



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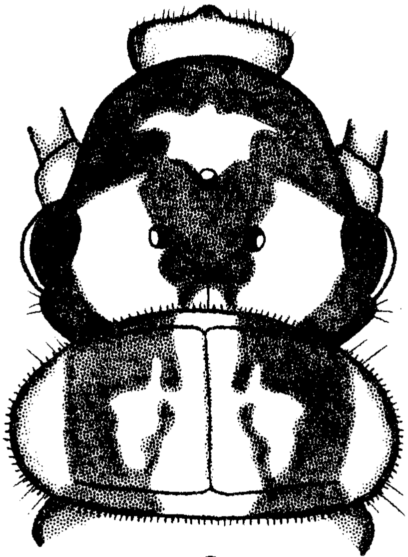

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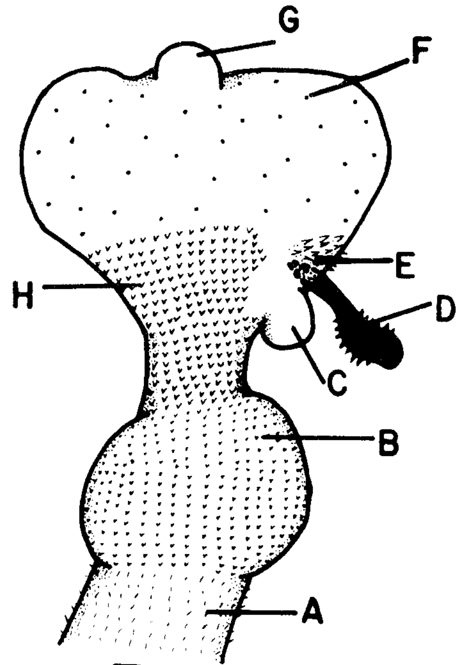

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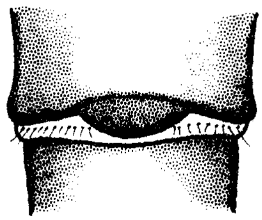

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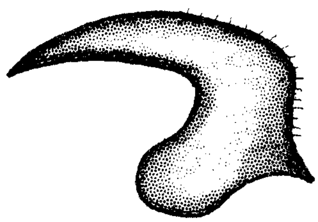

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process (Fig. 5E); small nipple below sclerotized process void of spinulae (Fig. 5C); mesal constricted section, bearing a dense wide band of small, stout spinulae (Fig. 5H); expanded, basal lobe covered with scattered, small spinulae (Fig. 5B); proximal stalk bearing scattered, small, fine, hair-like spinulae (Fig. 5A).

Female (Pl. XIV).-- Macropterous. Length of forewings 11-13 mm; length of body 10-13 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate of 8th sternum reduced, barely produced over anterior margin of 9th sternum, broadly rounded at posterior margin (Fig. 6).

Nymph (Reared) (Pl. XIV).-- Length of mature male nymph 9-10 mm; length of mature female nymph 11-13 mm. Dorsum of head with 3 light yellow patches, one anterior to forward ocellus, and 2 between compound eyes and lateral ocelli. Interocellar space dark; occipital ridge of spinulae absent (Fig. 2). Pronotum with median yellow stripe separating 2 wide, dark brown lateral longitudinal bands; each band partially enclosing variable patch of yellow; margin fringed with evenly spaced small stout setae, occasional long setae interspersed at upper and lower angles (Fig. 2). Meso- and metanota with 2 wide lateral and 2 thin mesal dark brown longitudinal stripes. Femora with stout spine-like setae on dorsal margin, and interspersed on outer surface; tibia with dorsal fringe of long, fine hairs, tarsi with few scattered, dorsal, fine hairs. Abdominal terga with 3 longitudinal stripes, 2 wide, dark brown lateral stripes, and one narrow, median, light brown stripe. Posterior margin of cercal segments with whorl of small stout setae, one medium-length ventral hair at posterior margin each segment after 13th.

Ova (Pl. XV).-- General shape oval, cross section circular (Fig. I). Color medium brown. Length .30 mm; width .20 mm. Collar developed and expanded slightly at apex with outer partitions (Figs. 1 & 2). Chorion with elevated thickened ridges forming hexagonal-shaped depressions bearing 9-14 evenly spaced punctations (Figs. 1-3). Micropyles arranged in pairs on top of ridges near bottom 1/3 on one side (Fig. 3).

Material examined.-- TYPES: Holotype ♀, NEVADA: Washoe Co., Reno, 1878, Morrison (CU #1,166). Allotype ♂, OREGON: Clackamas Co., Eagle Crk., 16/IV/1940, S. G. Jewett (CAS). Additional specimens - USA - CALIFORNIA: Butte Co., Chico, Richardson Springs, 5/IV/1962, S. G. Jewett, 6♂, 9♀, 7 exuviae (SJ); Fresno, 10 mi. N.E. of Academy, Dry Crk., 10/IV/1955, D. L. Abell, 2♂, 1♀ (SJ); Plumas Co., Grayeagle Crk., 8/VI/1965, S. G. Jewett, 4♂ (RWB). OREGON: Benton Co., Fishierier Lab, Oak Crk., 28/V/1977, S. W. Szczytko and K. W. Stewart, 1♀ (SWS & NTSU), Tampluko, 9 mi. N.W. of Corvallis, Berry Crk., 28/V/1977, S. W. Szczytko and K. W. Stewart, 1♀, 1 exuvia, 3 nymphs (SWS & NTSU); Corvallis, Oak Crk., 22/IV/1969, C. D. Kerst, 1♂ (SJ), Corvallis, Site 2, Oak Crk., 22/V/1969, C. D. Kerst, 3♀ (OS[2]), 9 mi. N.W. of Corvallis at Blacklight, Berry Crk., 20/VI/1968, C. D. Kerst, 1♀ (OS[2]), 4 mi. W. of Philomath, 27/IV/1963, 27/IV/1963, T. Schuh, 1♀ (USNM), Philomath, Woods Crk., 15/V/1936, V. E. Starr, 1♀ (WR), Corvallis, Site 2, Oak Crk., 10/V/1969, C. D. Kerst, 7♀ (OS[2]); Clackamas Co., Eagle Crk., 16/VI/1940, S. G. Jewett, 4♂, 1♀ (SJ), Eagle Crk., 5/V/1940, S. G. Jewett, 3♂, 3♀ (LCMNH); Clatsop Co., Red Bluff, Nehalem R., 25/VI/1965, S. G. Jewett, 1♂, 1♀ (RWB), Klatskanine R., 12/VI/1948, S. G. Jewett, 1♂ (SJ); Columbia Co., Beaver Crk., 17/IV/1954, S. G. Jewett, 1♂ (UU), Keasy, Rock Crk., 23/V/1954, S. G. Jewett, 1♂ (RWB); Washington Co., near Timber Junct., Wolf Crk., 1/VII/1967, S. G. Jewett, 1♂, 5♀ (INHS). WASHINGTON: Grays Harbor Co., Upper Wynoochie R., 29/V/1977, S. W. Szczytko and K. W. Stewart, 3♂, 3♀, 3 exuviae (SWS & NTSU).

Distribution.-- USA: California, Nevada, Oregon and Washington (Fig. VII).

Diagnosis and Discussion

This species is similar to *I. fulva*. Males can be distinguished by the lighter pigment patterns of the head pronotum, fumose anal area of hindwings, longer more acute paraprocts, and the following aedeagal characters: 1. general capitate shape; 2. clavate shape and dorsal-ventral spinulation of sclerotized process; 3. expanded, spinulated large lobe beneath constricted mesal section; 4. proximal stalk with scattered, small fine hair-like spinulae; and 5. absence of 2 long anterior tubular lobes. Females can be differentiated by the lighter pigment patterns of the head and pronotum, fumose anal area of hindwings, and often by the more shallow subgenital plate (in several specimens of I. fulva from Utah and Montana the shape of the subgenital plate is very similar). Nymphs can be separated by the lack of occipital ridge bearing spinulae, medium-length ventral hair at posterior margin of cercal segments after 12th segment, and 4 dark brown longitudinal stripes on meso- and metanota. Ova can be separated by the larger size, thinner chorionic ridges, and larger punctations.

Sheldon and Jewett (1967) reported that I. marmorata was a rare stonefly in the fauna of a Sierra Nevada stream emerging in early Jun. Kerst and Anderson (1974) found that emergence extended from late May until late Jul. in Oak Crk., Benton Co., Oregon. Material examined in this study had emerged from early Apr. until mid-Jun., beginning in southern latitudes and lower altitudies.

This is apparently a rare species and no studies have been don on its life history or general biology.

Isoperla fulva Claassen

Isoperla fulva, Claassen, 1937, 69:80. Holotype ♂, and allotype ♀; Logan R., Cache Co., Utah, USA (CU #1,687), (adult head and pronotum, male and female genitalia).

Isoperla chrysannula, Hoppe, 1938, 4:156. Holotype ♂, Shelton, Washington, USA (TBM); (male genitalia). Syn. Frison, 1942.

Isoperla cascadensis, Hoppe, 1938, 4:158. Holotype ♂, and allotype ♀, Tokul Crk., Washington, USA (TBM); (male and female genitalia). Syn. Frison, 1942.

Isoperla fulva, Claassen, 1940, 232:200.

Isoperla fulva, Frison, 1942, 22:337. Syn. indicated.

Isoperla fulva, Illies, 1966:403.

Isoperla fulva, Zwick, 1973:245.

Additional references: Isoperla fulva, Knowlton and Harmston, 1938; Ricker, 1939, 1943 (nymphal description, habitus female nymph, and maxilla); Gaufin, 1955; Jewett, 1959, 1960 (male and female genitalia); Knight and Gaufin, 1965, Knight et al., 1965a (ova); Knight and Gaufin, 1966, Nebeker and Gaufin, 1966, Gaufin et al., 1966 (adult mesosternum, wings, male and female genitalia and aedeagus); Knight and Gaufin, 1967; Newell, 1970; Richardson and Gaufin, 1971; Baumann, 1971; Gaufin et al., 1972 (wings, male and female genitalia); Stewart et al., 1974, Ricker and Scudder, 1975; Baumann et al., 1977 (adult mesosternum, ova, wings, male and female genitalia, and aedeagus); Fuller and Stewart, 1977.

Description (Plates XV and XVI)

Male (Pl. XVI).-- Macropterous. Length of forewings 8-9 mm; length of body 8-9 mm. General body color medium to light brown. Ocelli of head and bases antennae by dark brown "M"-shaped pigment band; median, quadrangular light brown spot behind lateral ocelli; interocellar space light (Fig. I). Pronotum light brown, median yellow stripe, rugosities dark brown (Fig. I). Wings fumose, veins medium brown. Femora, tibiae and tarsi medium brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Paraprocts short, stubby, not recurving over 10th tergum (Figs. 6 & 8). Cerci with long ventral hair at posterior margin each segment, one medium-length dorsal hair at posterior margin of segments 1-11. Vesicle shallow, broadly rounded, darker than rest of segment (Fig. 2). Aedeagus with large conical, posterodorsal lobe of small stout spinulae bearing clavate (lateral view) apical sclerotized process; tips of process pale, ladle-shaped, bearing long, stout spinulae (Fig. 4F); patch of long, stout spinulae anterior to process insertion (Fig. 4E); anterodorsal portion of aedeagus with large conical lobe void of spinulae (Fig. 4D); 2 long, narrow, membranous tubular processes extending forward from base of antero-dorsal lobe (Fig. 4C), one small lobe below insertion tubular processes void of spinulae (Fig. 4B), entire aedeagal stalk and small band between conical lobes bearing small stout spinulae (Fig. 4A).

Plate XV. Scanning electron micrographs and light micrographs of *Isoperla* ova.*

Figs. 1-3. *I. marmorata*. 1. whole ova 200X. 2. detail of crown 1000X. 3. detail of chorion and micropyle 2000X.

Figs. 4-10. *I. fulva*. 4. detail of chorion with proteinaceous bodies 1000X. 5. whole ova 200X. 6. detail of collar 1000X. 7. light micrograph of whole ova with enveloping gelatinous membrane 80X. 8. light micrograph - detail of collar and enveloping gelatinous membrane 800X. 9. light micrograph - detail of gelatinous membrane at posterior end 800X. 10. detail of chorion and micropyles 1000X.

* magnifications represent original values before reduction of plates

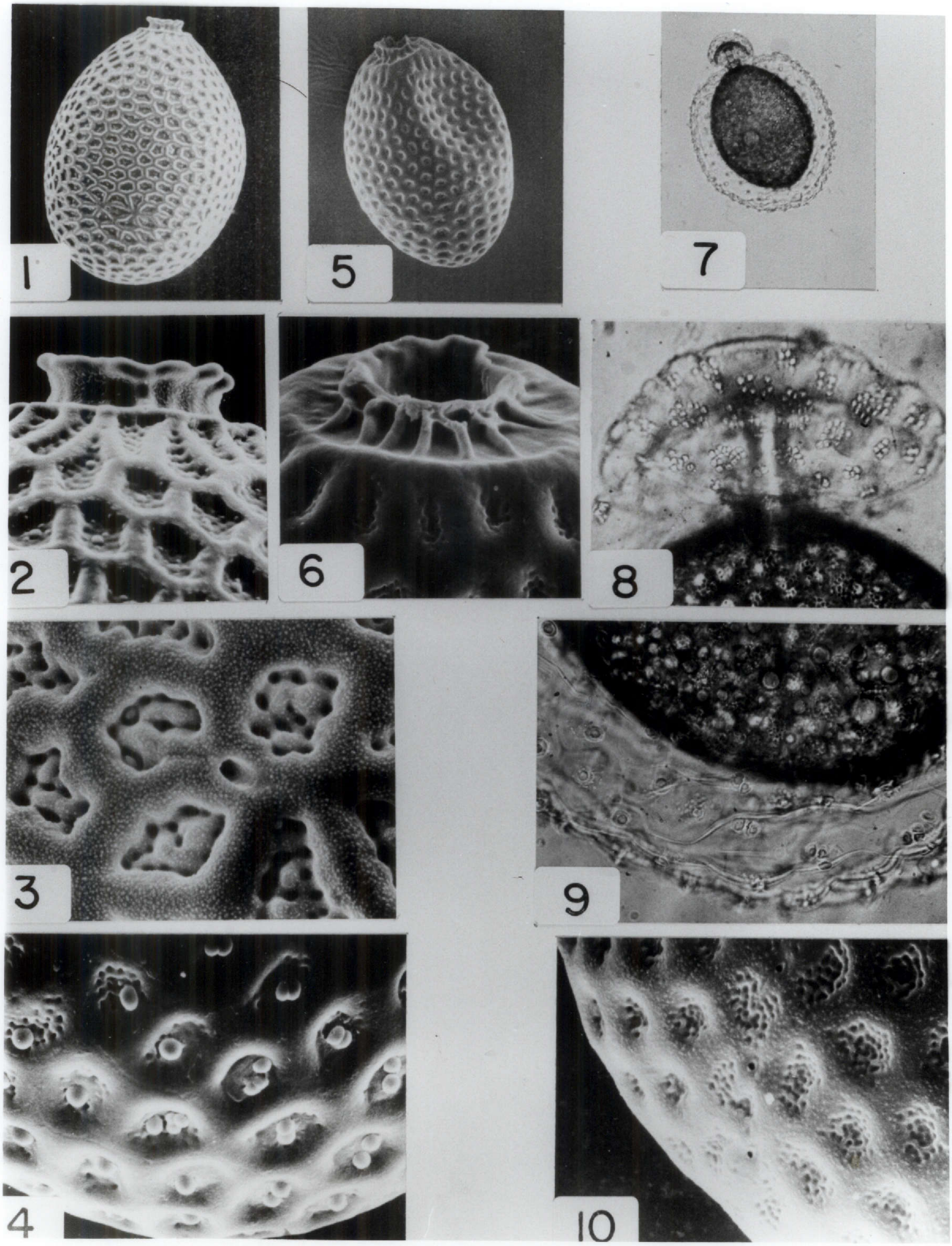
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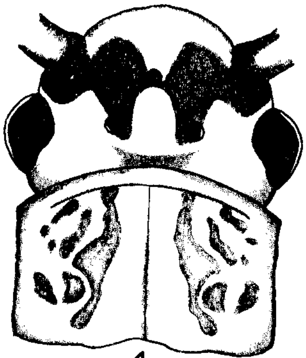
Plate XVI, Figs. 1-10. _I. fulva_. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. male vesicle and 8th sternum (1 mm = .05 mm). 3. nymph head and pronotum (1 mm = .10 mm). 4. male aedeagus, lateral aspect, A. band of small stout spinulae, B. small mesoanterior lobe void of spinulae, C. tubular processes, D. large anterodorsal conical lobe, E. patch of long stout spinulae, F. sclerotized process (1 mm = .03 mm). 5. female subgenital plate, typical (1 mm = .06 mm). 6. male terminalia, dorsal aspect (1 mm = .04 mm). 7. female subgenital plate, variation (1 mm = .06 mm). 8. male paraproct, lateral aspect (1 mm = .02 mm). 9. female vagina, A. vaginal armature, B. oviduct, C. subgenital plate, D. seminal receptacle, E. accessory receptacular glands (1 mm = .03 mm). 10. female subgenital plate, atypical variation (1 mm = .06 mm).



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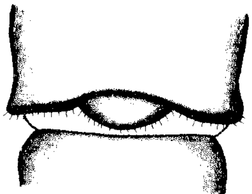

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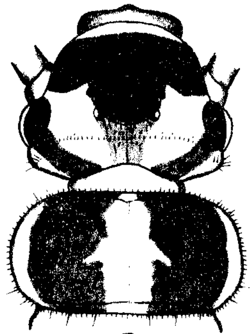

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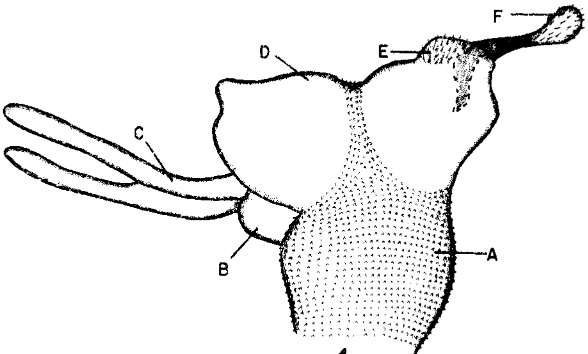

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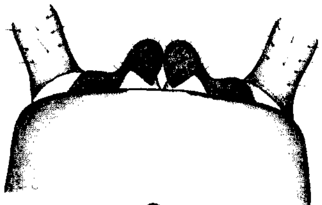

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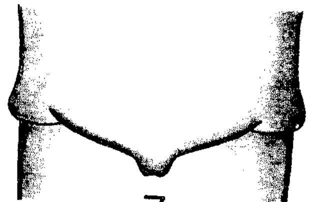

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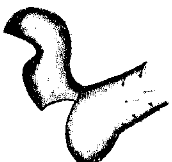

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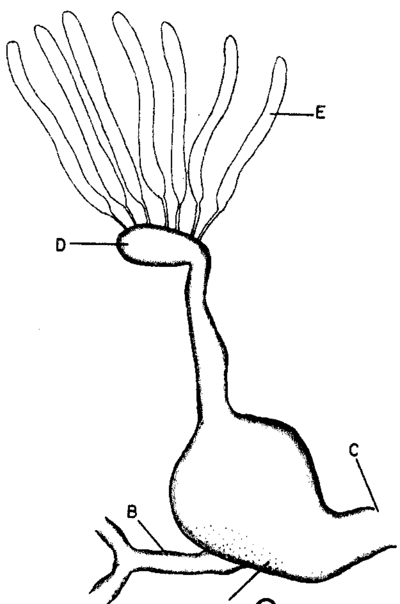

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10

Female (Pl. XVI).-- Macropterous. Length of forewings 10-11 mm. General body color, and head-pronotal pigment patterns similar to male. Subgenital plate variable, usually broad-angulate with simple or notched median nipple, produced posteriorly approximately 1/4 to 1/2 length of 9th sternum (Figs. 5 & 7); sometimes without nipple (Fig. 10).

Vagina with narrow ventral band of small stout spinulae (Fig. 9A), seminal receptacle (Fig. 9D) with 6-7 accessory receptacular glands (Fig. 9E).

Nymph (Reared) (Pl. XVI).-- Length of mature male nymph 11-12 mm; mature female nymph 13-15 mm. Dorsum of head with large "U"-shaped light yellow area between compound eyes; interocellar space and entire frons anterior to middle antennal bases dark (sometimes with light spot forward of median ocellus); dark band from each eye to occiput; occipital ridge with scattered small, fine spinulae (Fig. 3). Pronotum with median yellow stripe and lateral margins; rest dark brown; margin fringed with evenly spaced, small, stout setae, occasional long setae interspersed at upper and lower angles and posterior margin (Fig. 3). Femora with light dorsal fringe of long hairs and outer surface covered with spine-like setae; tibiae with heavy dorsal fringe of long hairs; ventral margin with row of medium-length hairs and ventral row of short, stout setae. Abdominal terga with 3 longitudinal stripes, 2 wide, dark brown lateral stripes and one narrow median light brown stripe. Posterior margin of cercal segments with whorl of small stout setae.

Ova (Pl. XV).-- General shape oval, anterior 1/2 always dented, cross section posterior 1/2 round (Fig. 5). Color medium brown. Length .26 mm; width .19 mm. Collar developed, depressed at base, with outer partitions (Figs. 5 & 6).

Material examined.-- TYPES: *I. fulva*, Holotype ♂, and allotype ♀, USA - UTAH: Case Co., Logan R., 17/VI/1926, J. G. Needham (CU #1,687). Paratypes, 1♂, 4♀, UTAH: Cache Co., Logan R., 15/VI/1926, J. G. Needham (CU #1,687). *Isoperla chrysannula*, Holotype ♂, and allotype ♀, USA - WASHINGTON: Tokul Crk., 16/V/1931, G. N. Hoppe (TBM). Paratypes, WASHINGTON: King Co., Snoqualmie, Snoqualmie Falls, 24/IV/1931, G. N. Hoppe, 1♂, Snoqualmie, 2/IV/1932, G. N. Hoppe, 1♂, 2♀ (TBM), Bothel, 13/IV/1931, G. N. Hoppe, 1♂ (TBM), Nisqually R., 30/IV/1931, G. N. Hoppe, 1♀ (TBM), Renton, 31/V/1913, Collector ?, 2♂, 1♀ (TBM). *I. chrysannula*, Holotype ♂, USA - WASHINGTON: Mason Co., Shelton, 29/IV/1931, G. N. Hoppe (TBM). Additional specimens - CANADA - ALBERTA, Waterton Lake, Kootenai R., 1/VIII/1970, A. R. Gaufin, 1♀ (UU); Waterton Lake, 23/VII/1923, J. McDonnough, 1♂, 1♀ (CU); BRITISH COLUMBIA, Veddar Crossing, Chilliwock R., 26/IV/1937, W. E. Ricker, 20♂, 6♀, 60 nymphs (INHS), Cutlus Lake, 1937,

W. E. Ricker, 1♂, 1♀ (INHS), Veddar Crossing, 9/V/1937, W. E. Ricker, 4♂, 2♀ (WR), Lakelse R., 15/VI/1950, F. Neave, 1♀ (WR), near Falls Wells, Gray Park, Clearwater R., 11/VII/1957, W. E. Ricker, 2♂, 3♀ (WR), Veddar Crossing, 14/VI/1957, W. E. Ricker, 4♂, 5♀ (WR), Cutlus Lake, Hatchery Crk., 31/III/1937, W. E. Ricker, 1 nymph (WR), Big Qualieum, 3 mi. below Horne Lake, 24/V/1953, W. E. Ricker, 9♀, 3 exuviae (WR). USA - CALIFORNIA: Plumas Co., N. Fork Feather R., Elv. 2,300 feet, 11/XI/1954, P. Chandler, 1♀ (SGJ). COLORADO: Archuleta Co., Hwy. 84, Toponas Crk., 26/VI/1962, Collector ?, 3♀ (UU); Unknown Crk. 2 mi. W. of Big Rock Crk. Hwy. 84, 26/VI/1962, Collector ?, 1♀ (UU), Hwy. 84, Big Rock Crk., 26/VI/1962, A. R. Gaufin, 5♂ (UU); Beaverhead Co., Dillon, Hwy. 6, Blue R., 30/VII/1960, Collector ?, 1♀ (UU); Chaffee Co., Hwy. 24, Granite, Arkansas R., 12/VII/1961, Collector ?, 3♂, 5♀ (UU), 10 mi. W. of Buena Vista, Cottonwood Lake, 30/VI/1974, S. J. Herman, 2♂, 2♀ (RWB); Conejos Co., Hwy. 17, 3 mi. E. of Lamanga Pass, Conejos R., 7/V/1976, S. W. Szczytko and K. W. Stewart, 4 nymphs (SWS & NTSU); EAgle Co., Hwy. 24 near Tennessee, EAgle R., 29/VI/1962, Collector ?, 37♂, 12♀ (UU), Hwy. 24 2 mi. S. of Camp Hale, Eagle R., 12/VII/1961, Collector ?, 7♂, 3♀ (UU), East Lake Crk., near Edwards, 29/VI/1962, Collector ?, 6♂ (UU), Hwy. 24 2 mi. S. of Camp Hale, Eagle R., 12/VII/1961, Collector ?, 5♂ (UU), Hwy. 24 near Tennessee, Eagle R., 29/VI/1962, Collector ?, 3♀

(UU); Grand Co., W. of Granby, Colorado R., 20/VI/1961, Collector ?, 4♀ (UU), Rocky Mt. National Park, Mill Crk., 27/VII/1960, A. R. Gaufin, 1♂ (UU), Hwy. 40 W. of Granby, Colorado R., 27/VI/1962, Collector ?, 10♂, 4♀ (UU), Rocky Mt. National Park, Fall R., 24/VII/1960, Collector ?, 1♀ (UU), W. of Granby, 20/VI/1961, A. R. Gaufin, 1 nymph (UU); Gunnison Co., 4 mi. above junct. with Gunnison R., Talor R., 12/VII/1962, Collector ?, 2♂ (UU), Lake Fort of Gunnison R., 5 mi. below Hwy. 149 at Roadside Park, 27/VI/1964, A. R. Gaufin, 2♂ (UU), Cebolla Crk., at junct. with Spring Crk., 13/VII/1962, Collector ?, 6♂, 2♀ (UU), W. Elk Crk. at Hwy. 50, 15/VI/1962, Collector ?, 4 nymphs (UU), W. Elk Crk., above Gunnison R., 20/VI/1962, A. R. Gaufin, 5 nymphs (UU), Soap Crk., 14/VI/1962, A. R. Gaufin, 4 nymphs (UU), Slate R. below Crested Butte, 12/VII/1962, A. R. Gaufin, 1 nymph (UU), Cebolla Crk. at junct. with Spring Crk., 13/VII/1962, A. R. Gaufin, 1 nymph (UU), 1/4 mi. above Hwy. 50 elevation 7,400 feet, E. Elk Crk., 20/IV/1962, Collector ?, 25 nymphs (UU); Hinsdale Co., 1/2 mi. above Lake San Cristobal, Lake Fort of the Gunnison R., 14/VII/1962, Collector ?, 2♂, 1♀ (UU), Lake Fort of the Gunnison R., 17/VI/1962, A. R. Gaufin, 61 nymphs (UU); La Plota Co., Lightner Crk. in Canyon, 4/IV/1961, A. R. Gaufin, 3 nymphs (UU); Larimer Co., Rocky Mt. National Park, Hidden Valley Crk., 24/VII/1960, Collector ?, 1♀ (UU); Mesa Co., Grand Mesa, stream at canyon 9,000 feet, 27/VI/1961, S. G. Jewett, 4♂, 4♀ (SGJ); Mineral Co., Wolf Crk. Pass, 21/VII/1938, D. J. and J. N. Knull, 291♂ (OS[2]); Montrose Co., Hwy. 50, Camarron Crk., 20/IV/1962, A. R. Gaufin, 1 nymph (UU); Park Co., 3 mi. N. of Como, Tarryall Crk., 8/VIII/1973, R. W. Baumann and B. P. Stark, 3♂, 2♀ (BS); Routt Co., Oak Crk., 22/VI/1968, B. R. Oblad, 4♂, 2♀ (UU), Beat R., 16/VII/1968, B. R. Oblad, 2♂, 5♀ (UU), Yampa, Yampa R., 19/VI/1961, A. R. Gaufin, 4♂, 3♀ (UU), Yampa, Yampa R., 22/VI/1968, B. R. Oblad, 6♀ (UU), Morrison Crk., 24/VI/1968, B. R. Oblad 1♀ (UU), Willow Cabins bridge, Yampa R., 22/VI/1968, B. R. Oblad, 2♂, 2♀ (UU), Green Crk., 16/VI/1968, B. R. Oblad, 1♀ (UU), Clark, Elk R., 17/VII/1968, B. R. Oblad, 1♂, 1♀ (UU), Big Crk., 18/III/1968, B. R. Oblad, 3 nymphs (UU), Steamboat Springs, Butcher Knife Crk., 18/III/1968, B. R. Oblad, 9 nymphs (UU), Hunt Crk., 18/III/1968, B. R. Oblad, 8 nymphs (UU), Trout Crk., 11/V/1968, B. R. Oblad, 1 nymph (UU), Yampa, Yampa R., 2/VI/1968, B. R. Oblad, 3 nymphs (UU), Hwy. 131 E. of Yampa,Yampa R., 26/VI/1962, Collector ?, 8♂, 1♀ (UU); Yampa Co., Yampa R., 19/VI/1961, Collector ?, 1♂ (UU); County ?, Webster, Aug., Oslar, 1♂ (CU). IDAHO: Bearlake Co., 1 mi. N. of Geneva Hwy. 89 elevation 6,350 feet,Salt Crk., 29/VI/1964, J. W. Richards and S. L. Jensen, 4♂, 3♀ (UU), Montrelier Crk., junct. Hwy. 89 elevation 6,200 feet, 29/VI/1964, J. W. Richardson and S. L. Jensen, 3♂, 4♀ (UU), Thomas Fork Crk. at junct. Hwy. 89 1/2 mi. N. of Geneva, 29/VI/1964,

, J. W. Richardson and S. L. Jensen, 1♀ (UU); Bonneville Co., Pine Crk. at junct. Hwy. 31 7 mi. N. Swan Valley elevation 5,900 feet, 21/VI/1964, J. W. Richardson and S. L. Jensen, 1♂ (UU); Boise Co., N. fork of Poytlo R. at Horseshoe bend, 17/VI/1964, Collector ?, 1♂ (UU), S. fork of Poyetlo R. at junct. with N. fork, 17/VI/1964, Collector ?, 2♂, 3♀, 1 exuvia (UU); Franklin Co., 1 mi. W. Mapleton at Sugar Crk. Bridge, Cub R., 20/VI/1964, J. W. Richardson and S. L. Jensen, 1♂, 2 nymphs (UU); Fremont Co., Head Worm R., 19/VI/1955, S. G. Jewett, 1♂ (UU); Gallatin Co., 3 mi. W. 3 Forks, Jefferson R., 2/V/1972, Roenhild, 2♂, 1♀ (TSU); Idaho Co., Warm R., 17/V/1952, S. G. Jewett, 4♂, 2♀ (SGJ), Lochsa R. at junct. with Selway R., 19/VI/1964, 2♂, 1 exuvia (UU), 8 mi. above Hwy. 13 on Hwy. H, S. fork of Clearwater R., 18/VI/1964, Collector ?, 1♀ (UU), junct. of stream with S. fork of the Clearwater R. 13 mi. below Elk City, 18/VI/1964, Collector ?, 1 nymph (UU); Lemhi Co., Salmon elevation 2,949 feet, 9/VI/1928, C. Wakeland, 3♂, 2♀ (CU), Hwy. 93 near Ellis, Salmon R., 19/VI/1964, Collector ?, 1♀ (UU), Hwy. 93 N. of Salmon, Bogle Crk., 17/VI/1965, A. R. Gaufin, 14♂, 10♀ (UU), N. fork of Salmon R., Hwy. 93, 18/VI/1964, Collector ?, 1♂, 1♀ (UU), Bogle Crk., Hwy. 93, N. of Salmon, 19/VI/1964, Collector ?, 9♂, 2♀ (RWB), N. fork of Salmon R., 17/VI/1965, A. R. Gaufin, 9♂, 7♀ (RWB), N. of Challis, Salmon R., 19/VI/1963, Collector ?, 1♂ (UU), 1 mi. N. of N. fork of Salmon R., 17/VI/1965, A. R. Gaufin, 7♂, 3♀ (UU); Teton Co., Teton R. at junct. Hwy. 33 2 mi. W. of Tetonia, 22/VI/1964, J. W. Richardson and S. L. Jensen, 1♂, 2♀ (UU), N. fork of Teton R. at junct. Hwy. 32, 22/IV/1964, J. W. Richardson and S. L. Jensen, 1 nymph (UU); County ?, W. fork of Madison R., 8/VIII/1972, Collector ?, 2♀ (ISU). MONTANA: Beaverhead Co., Dillon, Big Hale R. Hwy. 19 N., 16/VI/1967, A. R. Gaufin, 18♂, 7♀ (UU), 15 mi. S. of Dillon, Beaverhead R., 19/V/1965, A. V. Nebeker, 17♂, 10♀ (RWB), N. of Dillon, Beaverhead R., 16/VI/1967, A. R. Gaufin, 7♂, 18♀ (UU), Red Rock R., 28/VI/1973, G. F. and C. H. Edmunds, 5♂ (BS); Broadwater Co., 15 mi. E. of Townsend, Deep Crk., 8/VII/1966, J. R. Grierson, 1♀ (UU), Missouri R. Bridge at Toston, 11/V/1950, Collector ?, 5♂, 5♀ (UU), Toston, Missouri R. Bridge, 8/V/1949, R. Hays, 5♂, 2♀, 3 nymphs (UU); Carson Co., E. Rosebud Crk., 21/VI/1966, J. R. Grierson, 4♂, 1♀ (UU); Cascade Co., Belt Crk., 7/VII/1966, Collector ?, 2♂ (UU); Fergus Co., Big Spring Crk., 16/IV/1952, N. A. Thoreson, 10♂, 5♀ (UU); Flathead Co., N. fork of Flathead R., 7/VII/1973, J. Stanford, 3♂, 2♀ (JS), Bowman Crk., 24/VII/1970, A. R. Gaufin, 2♀ (UU), N. fork of Flathead R. at Stat. 5, 7/VII/1973, J. A. Stanford, 3♂, 2♀ (JS); Gallatin Co., W. Gallatin R., 6/VII/1951, R. Hays and J. Bailey, 1♀ (UU), W. Gallatin R., 13/VI/1951, Collector ?, 24♂, 15♀ (UU), Bozeman, Hoffman Crk., 20/VI/1950, R. Hays, 4♂, 1♀ (UU), Hwy. 191 near Baconrind, W. Gallatin R., 26/VII/1963, A. R. Gaufin, 12♂, 8♀ (UU), Hyalite Crk., 3/VIII/1950, Collector ?, 2♀ (UU), Madison R. above Hebgen Lake, 24/VI/1964, J. W. Richardson and S. L. Jenson, 4 nymphs (UU); Glacier Co., Glacier National Park, St. Mary's R. at St. Mary's Campground, 30/VII/1965, A. R. Gaufin, 2♀ (UU), Hwy. 89 E. of Glacier Park, Cutbank Crk., 22/VII/1966, A. R. Gaufin, 1♀ (UU), Cutbank Crk., 18/VII/1965, A. R. Gaufin, 1♀ (UU), Hwy. 89 near Babb, St. Mary's R., 23/VII/1966, A. R. Gaufin, 2♂, 5♀ (UU), St. Mary's Campground, St. Mary's R., 10/VII/1964, A. R. Gaufin, 4♂, 1♀ (UU), entrance to Glacier National Park, Sherrburne Crk., 7/VII/1966, A. R. Gaufin, 3♂, 6♀ (UU), St. Mary's Campground, St. Mary's R., 23/VII/1966, A. R. Gaufin, 16♂, 28♀ (UU); Granite Co., Hwy. 10A near Phillipsburg, Flint Crk., 16/VI/1967, A. R. Gaufin, 18♂, 8♀ (UU), Flint Crk., Hwy. 10A near Phillipsburg, 16/VI/1967, A. R. Gaufin, 18♂, 6♀ (UU), Stoney Crk., 28/VI/1967, M. L. Miner, 15♂, 7♀ (RWB), Rock Crk., 28/VI/1967, R. L. Newell, 26♂, 17♀ (UU), Hwy. 10A near Phillipsburg, Flint Crk., 16/VI/1967, A. R. Gaufin, 20♂, 10♀ (UU), Rock Crk., 4/IV/1969, B. R. Oblad, 11 nymphs (UU); Judith Basin Co., Judith R., 2/VIII/1967, J. R. Grierson, 1♂, 1♀ (UU), Arrow Crk., 7/VII/1966, J. R. Grierson, 1♀ (UU); Lake Co., Hwy. 209, Leon Crk., 24/VI/1964, A. R. Gaufin, 5♂, 3♀ (UU); Lewis and Clark Co., Hwy. 20 E. of Bonner, Blackfoot R., 23/VII/1967, A. R. Gaufin, 28♂, 26♀ (UU), Keepcool Crk., 1/VII/1969, R. L. Newell, 5♂, 2♀ (UU);

Meagher Co., 15 mi. above Smith R., Thomas Crk., 8/VII/1966, J. R. Grierson, 1♂, 1♀ (UU), Sheep Crk., 7/VII/1966, J. R. Grierson, 1♂ (UU), 2 mi. N. of White Sulphur Springs, Smith R., 8/VII/1966, J. R. Grierson, 2♂, 1♀ (UU), Clearwater R., Alva Lake outlet, 1/VII/1969, R. L. Newell, 2♀ (UU), Spring Crk., 1/VII/1966, J. R. Grierson, 1♂, 1♀ (UU); Missoula Co., Warm Spring Camp, Bitterroot R., 19/VII/1963, Collector ?, 1♂, 1♀ (UU), Blackfoot R., 8/VII/1969, R. L. Newell, 1♂, 6♀ (UU), 16.4 mi. above Hwy. 93, Lolo R., 16/VII/1965, J. R. Grierson, 2♀ (UU), 17 mi. above Bitterroot R., Miller Crk., 20/VII/1965, J. R. Grierson, 1♀ (UU), 5 mi. W. of Lolo, Lolo R., 29/VI/1964, A. R. Gaufin, 35♂, 24♀ (UU); Park Co., Shields R., 1/VII/1966, J. R. Grierson, 6♂, 4♀ (UU); Powell Co., Montura Crk., 1/VII/1969, R. C. Newell, 4♂ (UU), Hwy. 200, Montura Crk., 11/VI/1970, A. R. Gaufin, 2♀ (UU); Ravalli Co., Woodside, Bitterroot R., 18/V/1955, D. R. Mariekey, 6♂, 2♀ (UU), above E. fork, Bitterroot R., Camp Crk., 22/VI/1965, J. R. Grierson, 1♀ (UU), E. fork of Bitterroot R. 10 mi. above junct. with W. fork, 28/VI/1965, J. R. Grierson, 1♂, 2♀ (UU), 1 mi. above Hwy. 93, Warm Springs Crk., 24/VII/1965, J. R. Grierson, 1♀ (UU), E. fork of Bitterroot R. 10 mi. above j-nct. with W. fork of Bitterroot R., 22/VI/1965, J. R. Grierson, 2♂, 3♀ (UU), Hwy. 93, Warm Springs Camp, Bitterroot R., 29/VII/1963, Collector ?, 3♂, 1♀ (UU), E. fork of Bitterroot R. at Sulo Post Office Hwy. 93, 27/VI/1964, A. R. Gaufin, 1♂, 3♀ (UU), Camp Crk., 22/VI/1965, J. R. Grierson, 1♂, 1♀ (UU), S. fork of Bitterroot R. at Sulo Ranger Station, 27/VI/1964, A. R. Gaufin, 3♂, 6♀ (UU); Sanders Co., Hwy. 93 N. of Jocko Camp, 2 mi. S. of Ravalli, Jocko R., 20/VI/1963, A. R. Gaufin, 14♂, 9♀ (UU); Stillwater Co., Stillwater R., 25/VI/196-, J. R. Grierson, 5♂, 2♀ (UU); Sweet Grass Co., 21 mi. S.W. of Big Timber, Boulder R., 28/VI/1966, J. R. Grierson, 15♂, 6♀ (RWB), Sweet Grass Canyon above Hwy. 19, 30/VI/1966, J. R. Grierson, 1♂, 2♀ (UU), Bridger Crk., 24/VI/1966, J. R. Grierson, 4♂, 1♀ (UU); County ?, Babb, Swift Crk., 13/VII/1963, Collector ?, 2♂, 3♀ (UU), Potomac, Big Blackfoot R., 20/VI/1966, F. E. Barry, 1♂, 1♀ (CU). NEVADA: Eklo Co., Hwy. 11, Secret Crk., 15/VI/1974, B. P. Stark, 15♀ (BS), Secret Crk. at Secret Pass, 15/VI/1974, B. P. Stark, 9♂, 5♀ (BS). NEW MEXICO: Colfax Co., Cimarron Canyon, Ute Park, 12/VI/1956, Collector ?, 1♂ (WR); San Miguel Co., near Terrero, Holy Ghost Crk., 19/VI/1961, S. G. Jewett, 4♂ (SGJ); Taos Co., Panchuela near Cowler, 9/VII/1944, W. J. Coster, 1♂ (WR). OREGON: Clackamas Co., Big Eddy, 1/VI/1952, S. G. Jewett, 7♂, 5♀ (LCMNH), Hwy. 26 at Brighton, Salmon R., 24/VI/1967, R. W. Baumann, 1♂, 5♀ (RWB); Clatsop Co., Big Crk., 16/IV/1949, S. G. Jewett, 2♂ (LCMNH), Young R., 13/IV/1947, S. G. Jewett, 2 nymphs (SGJ), Big Crk., 16/IV/1949, S. G. Jewett, 5 nymphs (SGJ), Grant Co., middle fork of John Day, 29 mi. S. of Ukian

Hwy. 395, 29/IV/1977, Dunster, 1♂, 1♀, 1 nymph (CWS); Jackson Co., 4 mi. W. Dead Indian, Soda Spring, 21/V/1964, J. Schuh, 1♂, 1♀ (CU); Lake Co., Chewaucan R. dam site, 18/VI/1955, J. Schuh, 1♀ (OS^2), Chewaucan R., 18/VI/1955, J. Schuh, 1♀ (OS^2); Modoc Co., Pit R., 28/IV/1977, Dunster, 2♀ (CWS); Wallowa Co., Minam, Wallowa Canyon Fount., 21/VII/1929, H. A. Scullen, 1♂ (CU); County ?, Burnt R., near Lime, 20/IV/1954, W. Ricker, 5♂, 1♀, 5 exuviae (WR), Rock Crk. E. of Miteil, 6/V/1970, S. G. Jewett, 2♂, 1♀ (SGJ). UTAH: Boxelder Co., 5 mi. E. Brigham City, Boxelder Crk., 29/VI/1952, C. J. D. Brown, 1♀, 1 nymph (UU); Cache Co., Logan, 23/VI/1907, E. G. Titus, 1♀ (CU), Logan Canyon, 27/VI/1937, W. P. Nye, 1♂, 1♀ (SWS & NTSU), Logan Canyon, Logan R., 18/VI/1960, G. F. Knowlton, 6♂, 3♀ (UU), Logan Canyon, 7/VII/1939, D. J. and J. N. Knull, 7♀ (OS^2), Logan R., 12/VII/1922, Collector ?, 1♂ (CU), Logan R., 26/VI/1926, Collector ?, 1♂ (CU), Logan R., 18/VI/1926, Collector ?, 1♂ (CU), Logan R., 16/VI/1926, Collector ?, 1♂, 1♀ (CU), Logan 4/VI/1903, Collector ?, 1♂ (CU), Logan Canyon, 7/IV/1966, W. P. Nye, 2♂, 4♀ (UU); Duchesne Co., Unita R. at Wandin Campground, 7/VIII/1975, R. W. Baumann, 2♂, 3♀ (RWB), Uinta Campground, Uinta R., 7/VIII/1975, R. W. Baumann, 2♂ (RWB); Emery Co., Ferron Picnic ground above Hwy. 10, Ferron Crk., 12/V/1976, S. W. Szczytko and K. W. Stewart, 6 nymphs (SWS & NTSU); Grand Co., Manti-La Sal National Forest, Hunting Canyon 2 1/2 mi. E. of Boulyar Camp, 3/VII/1949,

L. G. Gunderson, 3/VII/1949, 1♀ (UU); Lake Co., Swan R., 8/VII/1967, Milan, 24♀ (UU); Rich Co., Big Crk. above Randolph, 17/VI/1975, R. W. Baumann, 3♂ (RWB); Salt Lake Co., Mill Crk. Porter Fork, 1-/VI/1972, B. P. Stark, 1♀ (BS), Mill Crk. 1000 Springs, 16/VI/1972, B. P. Stark, 1♀ (BS), Big Cottonwood Crk., 14/VII/1966, R. W. Baumann, 1♂, 2♀ (UU), Emigration Canyon Crk., 12/VI/1966, R. W. Baumann, 25 nymphs (RWB), Church Fork Mill Crk., 16/VI/1972, B. P. Stark, 1♂, 1♀ (BS), Little Dell Crk., 17/VI/1965, R. W. Baumann, 1♂ (UU), Big Cottonwood Crk. at Silver Fork, 14/VII/1966, R. W. Baumann, 1♀ (UU), Mill Crk. Canyon Crk., 9/VI/1966, R. W. Baumann, 4♂, 2♀ (RWB), American Forks Canyon, Date ?, Hubard and Schwarz, 1♂ (CU), Parley's Crk. above Mt. Dell, 5/VI/1963, A. V. Nebeker, 2 nymphs (UU), Emigration Canyon Crk., 2/V/1966, R. W. Baumann, 1 nymph (UU), Mill Crk. Canyon Crk., 15/V/1965, R. W. Baumann, 5 nymphs (UU), Mill Crk. Canyon Crk., 11/IV/1966, R. W. Baumann, 1♂, 8♀, 3 nymphs (SGJ), Little Dell Crk., 26/V/1965, R. W. Baumann, 9 nymphs (RWB), Cardiff Fork Bridge, Big Cottonwood Crk., 29/VI/1966, R. W. Baumann, 7♂, 1♀ (RWB), City Crk. near spring 1/4 mi. above caretakers, 29/III/1966, Uresh, 6 nymphs (UU); Summit Co., Silver Crk., 9/VI/1961, R. W. Baumann, 1♂, 2♀ (UU), Weber R., Middle Fork, 5/VIII/1975, Sakamoto et al., 2♀ (RWB), Weber R. near Oakley, 5/VII/1975, Sakamoto et al., 1♂ (RWB), W. F. Blocks Fork R., 4/VII/1975, R. W. Baumann, 1♂ (RWB), Provo

R. at Vivian Park, 2/VII/1954, A. R. Gaufin, 14♂, 10♀ (UU), Weber R. below Ploa, 17/V/1967, B. R. Oblad, 5 nymphs (UU), Brigham Canyon, 14/V/1937, Knowlton and Harmston, 1♂, 2♀ (INHS), Weber R. at Piney Resort, 23/I/1960, S. C. Jorgenson, 20 nymphs (UU), E. Canyon Crk. bridge 2 mi. above reservoir, 7/VII/1965, R. W. Baumann, 1♂, 12♀ (RWB); Utah Co., Provo R., 24/VII/1971, J. W. Aaron, 3♂, 1♀ (BYU), Dry Canyon Crk. at Hwy. 80, 7/IV/1966, R. W. Baumann, 7 nymphs (UU), American Fork Canyon, 15/IV/1967, B. R. Oblad, 16 nymphs (RWB); Weber Co., Ogden R. below Pine R. dam, 2/V/1968, R. W. Baumann, 8♂, 7♀ (RWB), Pine Valley, 28/VI/1937, D. J. and J. N. Knull, 1♀ (OS[2]), E. Canyon Crk. at Kimball junct. 15 E. of Provo, 13/V/1976, S. W. Szczytko and K. W. Stewart, 26 nymphs (SWS & NTSU). WASHINGTON: Rajumy R., 20/IV/1932, Collector ?, 1♀ (UW), Snoqualmie, 16/V/1931, Collector ?, 1 p (UW); Kittitas Co., Cle Ella, 15/VII/1932, D. R. Hoppe, 1♀ (UW), Ellensburg, Jakima R., 8/VIII/1882, S. Hendshaw, 1♂ (UW); Shamama Co., Mt. Adams Area, Lewis R., 31/VIII/1958, Collector ?, 1 nymph (UW); Thurston Co., Olympia, 2/VI/1895, Collector ?, 1♀ (CU); County ?, Nesquelly R., 2/V/1931, Collector ?, 1♀ (UW). WYOMING: Carbon Co., Medicine Bow Mts., Top of Pass, 14/VIII/1947, Ross and Ross, 1♂ (WR), Riverside, Madison R., 2/V/1964, Collector ?, 3 nymphs (UU); Lincoln Co., at junct., Hwy. 26 2 mi. N. of Smoot, Salt R., 29/VI/1964, J. W. Richardson and S. L. Jensen, 4♂, 3♀ (UU);

Park Co., S.E. of Cooks City, Clarks Fork of Yellowstone R., 28/VII/1966, J. R. Grierson, 1♂, 2♀ (UU), Cascade Camp, Yellowstone R., 6/VII/1951, A. R. Gaufin, 1♂ (UW); Sublette Co., N. of Cora, Willow Crk., 18/VII/1962, Collector ?, 1♂ (UU), Daniel, Green R., 19/VII/1972, B. P. Stark, 1♂ (BS), 21 mi. N. of Cora, Green R., 19/VII/1972, B. P. Stark, 2♂ (BS), Spider Web, Pine Crk. at Pinedale, 20/VII/1972, B. P. Stark, 1♂ (BS); Teton Co., junct. Hwy. 26 and 89, Hoback R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 5 nymphs (UU), 7 mi. N. of Jackson, Gros Ventre R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 11 nymphs (UU), 3 mi. S. of canyon junct., Yellowstone R., 26/VI/1964, S. L. Jensen and J. W. Richardson, 8 nymphs (UU), Grant Teton National Park, Snake R., 28/VI/1964, S. L. Jensen and J. W. Richardson, 2 nymphs (UU), Yellowstone National Park, 1921, J. T. Needham, 2♀, 1 nymph (CU), near Jackson, Hoback R., 6/VII/1936, H. H. Ross, 1♂, 5♀ (INHS), junct. Hwy. 26 and 187, 7 mi. N. of Jackson, Gros Ventre R., 23/VI/1964, S. L. Jensen and J. W. Richardson, 18♂, 16♀ (RWB), near Hoback junct., Snake R., 16/VI/1973, J. Perry, 2♂, 1♀ (RWB), Hwy. 167, Cliff Crk., 14/VII/1962, Collector ?, 1♂ (UU), Yellowstone National Park, Gibbon R., 25/VI/1964, S. L. Jensen and J. W. Richardson, 1♂ (UU), 10 mi. W. of Thumb, Yellowstone National Park, Crawfish Crk., 27/VII/1964, J. W. Richardson and S. L. Jensen, 5♂, 2♀ (UU), Moose, Grand Teton National Park, Snake R., 28/VI/1964, J. W. Richardson and S. L. Jensen, 1♂ (UU); County ?, Univ. of Wyoming Sci. Camp, Nash Fork Crk., VI/1960, A. F. Bogge, 2♂, 2♀, 6 nymphs (SJ). UNKNOWN LOCALITIES: County ?, 2 mi. above Ennis Lake, Madison R., 3/V/1970, Collector ?, 2♂, 3♀ (UU); Lake Co., Salmon Py. Swan R., 20/VII/1962, Milam, 4♀ (UU).

Distribution.-- CANADA: Alberta, British Columbia; USA: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (Fig. VII).

Diagnosis and Discussion

This species is very similar to *I. marmorata* (see diagnosis and discussion under *I. marmorata*). It is the most common western *Isoperla* in collections, from a wide range of lotic habitats.

Knight and Gaufin (1965) found that reducing dissolved oxygen concentrations to 1.0 cc/l, and water flow to 0.004 feet/sec. at 10^{o} C, killed 8 percent of *I. fulva* nymphs within 24 hours, and 100 percent within 144 hours. Knight and Gaufin (1966) reported that *I. fulva* was eurythermic and distributed between 7,000 to 9,200 feet in the Gunnison River drainage system in Colorado. It occurs in temporary streams, high elevation streams, low elevation streams, stony rivers, constant rivers, and sluggish rivers in the Gunnison River drainage system in Colorado, associated most frequently with *Sweltsa coloradensis* (Banks), *Isoperla patricia* ÷ *I. quinquepunctata* (Banks), *Hesperoperla pacifica*

(Banks), and _Claassenia_ _sabulosa_ (Banks) (Knight and Gaufin 1967).

Richardson and Gaufin (1971) reported that pre-emergent _I_. _fulva_ nymphs were primarily carnivores. Fuller and Stewart (1977) found that newly recruited _I_. _fulva_ nymphs in Oct. were primarily phytophagus, with filamentous algae comprising 47.5 percent, diatoms 15.5 percent, detritus 28 percent, and animal matter 9 percent of their diets. In Dec. the nymphs shifted toward carnivory, feeding increasingly on Chironomidae larvae and Ephemeroptera nymphs, and in May and Jun., pre-emergent nymphs fed primarily on Chironomidae larvae.

My examination of ova from live gravid females revealed that each punctation in the large chorionic depressions contained a rounded proteinaceous body (Pl. Fig. 4). These structures are undoubtedly shrunken by alcohol preservation and the dehydration techniques used in preparing ova for SEM study, and therefore do not appear in most of the photographs. When placed in water these bodies spring out, pushing a gelatinous sticky membrane away from the surface, that when fully expanded completely surrounds the ova and offers adhesion to substrates (Figs. 7-9). The patterns of punctations can be observed in the expanded gelatinous membrane (Figs. 7-9). About 2 and one-half min. in water were required for full development of the envelope.

Stanford (unpublished Ph.D dissertation) found that *I. fulva* in the upper Flathead River, Montana exhibited a univoltine life cycle, with emergence occurring from late May until early Jul. Nymphs first appeared in the river in late Jul.

Adults from the extensive material examined emerged in early May-Aug., with the largest numbers taken from mid-Jun. to early Jul. It is the most common western *Isoperla*, from the widest range of lotic habitat types.

Species Group E

Isoperla sordida complex

This group is composed of *I. acula* Jewett, *I. adunca* Jewett, *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett, *I. sordida* Banks, and a new species, *I. bifurcata*. These species all share the following characteristics: 1. long ventral hair at posterior margin of adult cercal segments; 2. male aedeagus with variable sclerotized process, bifurcate at base; 3. well-developed, variable-shaped male vesicle; 4. variable female subgenital plate, usually with a median emargination; 5. short stout hairs and an occasional long hair on margin of nymphal pronotum; 6. chorionic ridges of ova variable and usually well developed; and 7. chorion covered with small punctations.

The sclerotized process of the male aedeagus exhibits a distinct phenocline (Pl. XVII). The base of the process is forked in all species, and the dorsal arm is variously modified from a simple short rod to an elongate forked or unforked process. In _I_. _adunca_ the process is very short, and the simple dorsal arm is narrow and slightly expanded at its apex (Pl. XVII, Fig. I: Pl. XIX, Fig. 4D). In _I_. _rainiera_ the process is short and stout, with a broad dorsal arm bearing 2 lateral downward projecting spines (Pl. XVII, Fig. 2; Pl. XXVI, Fig. 5 & 4D). The dorsal arm of _I_. _denningi_ is elongated, with a slight median emargination at the apex (Pl. XVII, Fig. 3; Pl. XXII, Figs. 3 & 5C), and in _I_. _sordida_ it has become constricted in the middle and expanded at the base and apex, forming 2 rounded lobes apically bearing short, stout spinulae on the outer margin (Pl. XVII, Fig. 4; Pl. XXVII, Figs. 3, 4E, & 7). In _I_. _bifurcata_ the dorsal arm is forked near the base-arm plate and near its midsection, forming 2 moderately long apical arms bluntly pointed at the tips, and each bearing a ventral spine (Pl. XVII, Fig. 5; Pl. XXI, Figs. 4C & 7). The forked members of the _I_. _fusca_ dorsal arm are curved, very long, and tapered to fine points which cross near the apex; each arm bears a curled ventral spine near the bottom 1/3 of its length (Pl. XVII, Fig. 4; Pl. XXIII, Figs. 5 & 7C). In _I_. _petersoni_ the dorsal arm members have apparently fused into a single long, curved, striolate, needle-like process (Pl. XVII, Fig. 7; Pl. XXV, Fig. 4C). Placement

Plate XVII, Figs. 1-7. Phenocline of sclerotized aedeagal structure in the *I. sordida* species complex. 1. *I. adunca*, 2. *I. rainiera*, 3. *I. denningi*, 4. *I. sordida*, 5. *I. bifurcata*, 6. *I. fusca*, 7. *I. petersoni*.

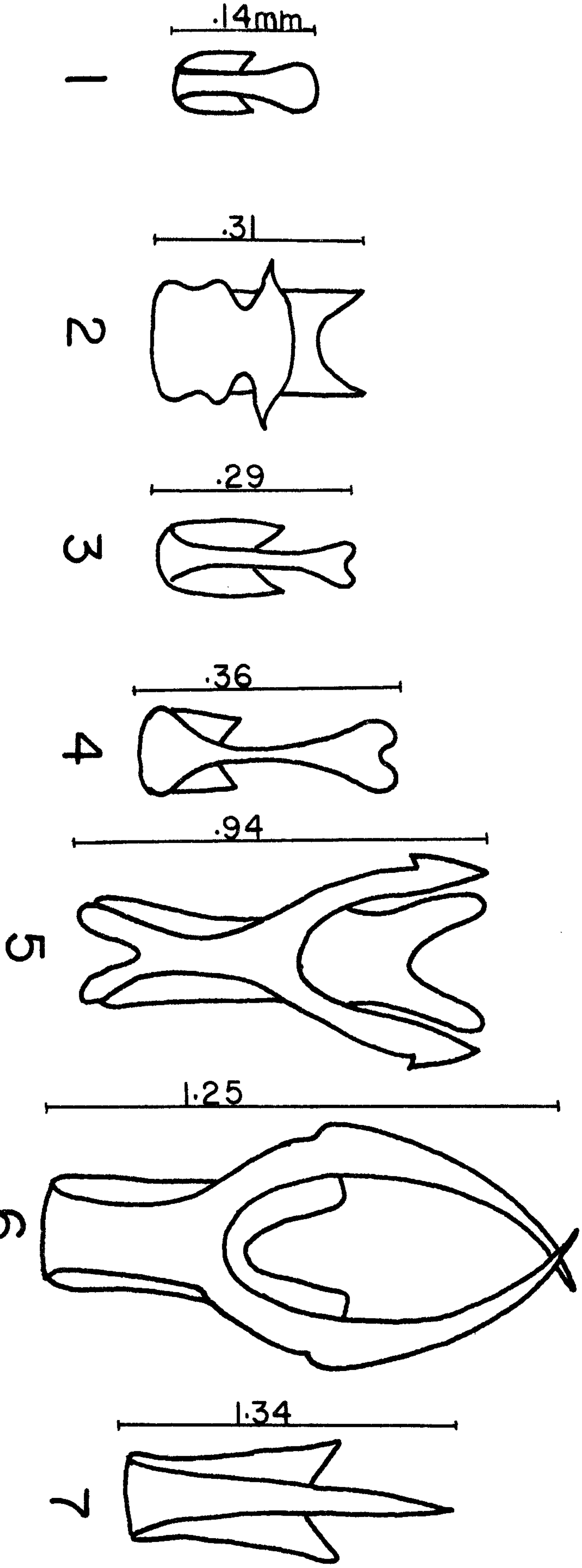
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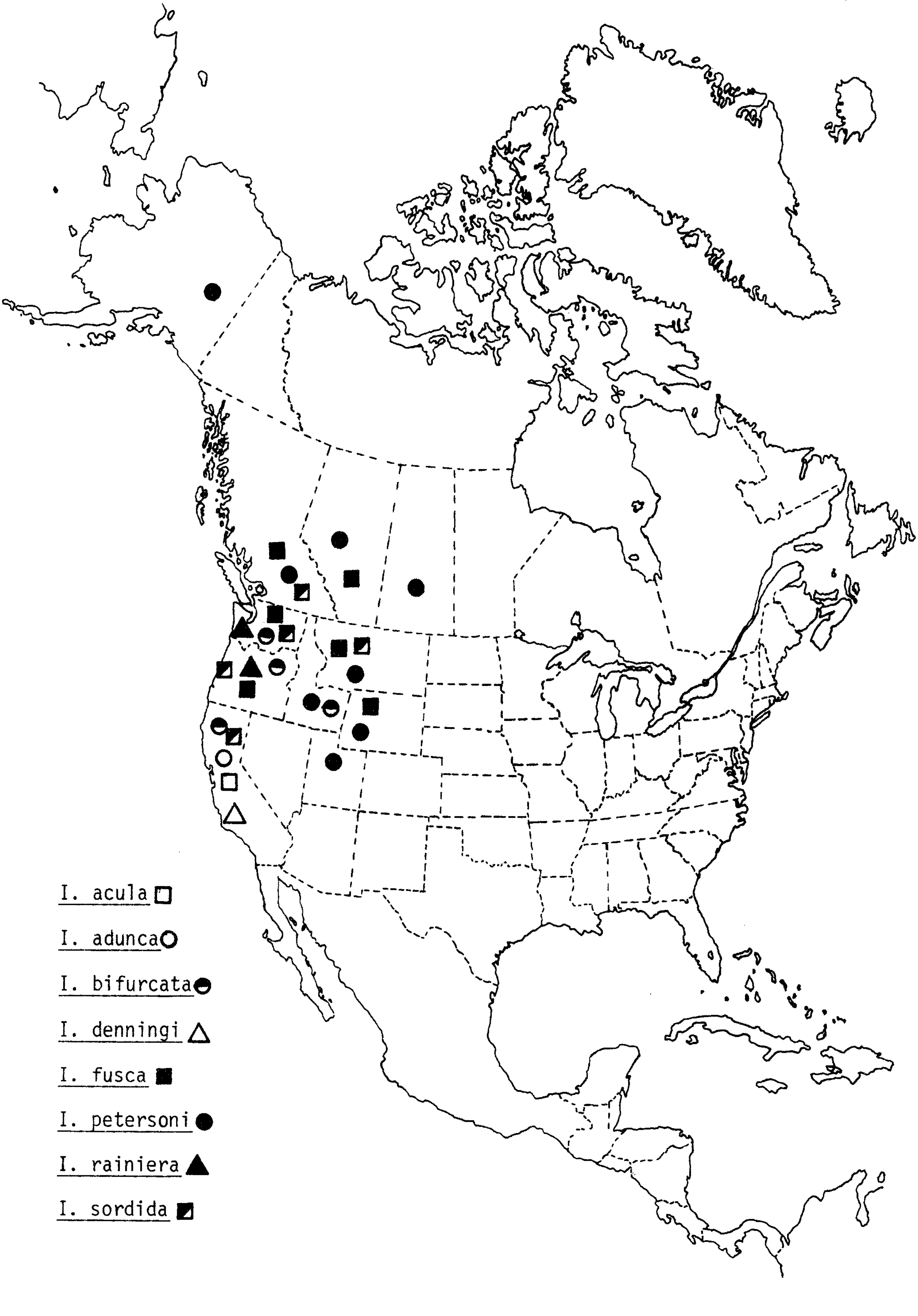
Fig. VIII. Distribution of the *I. sordida* complex


I. acula
I. adunca
I. bifurcata
I. denningi
I. fusca
I. petersoni
I. rainiera
I. sordida

of *I. petersoni* at this position in the phenocline was also based on the similarity of its ova with *I. fusca*.

This group is concentrated in the western coastal mountain ranges and Northern Rocky Mountains, with one record of *I. petersoni* from Alaska (Fig. VIII). Most species inhabit small creeks or springs. Emergence occurs from Apr.-late Oct., and all species probably undergo univoltine life cycles.

Isoperla acula Jewett

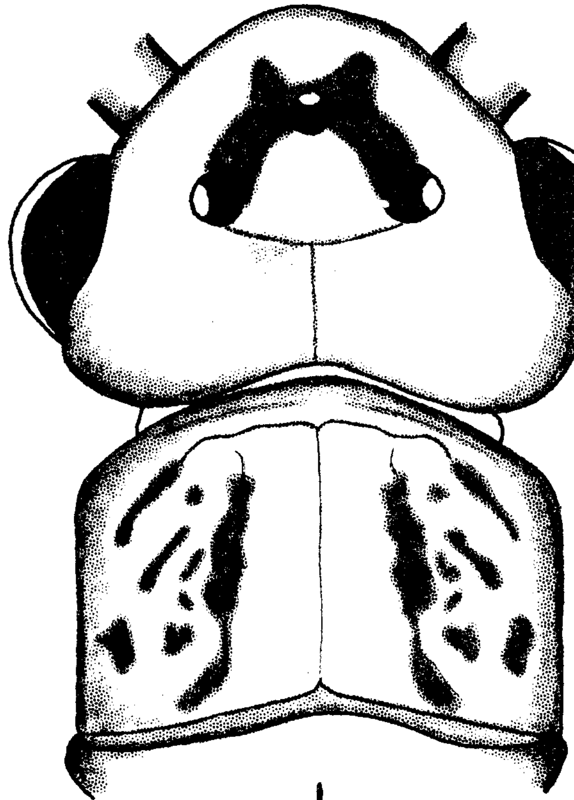
Isoperla acula Jewett, 1962, 38:18. Holotype P; 7 mi. N.E. of Academy, elevation 800 feet, Fresno, Co., California, USA (CAS) (male genitalia, and head-pronotal pattern).

Isoperla acula, Illies, 1966:393.

Description (Plates XVIII and XX)

Male (Pl. XVIII).-- Macropterous. Length of forewings 9-10 mm; length of body 9-10 mm. General body color light brown. Ocelli of head connected by narrow band of dark brown pigmentation; interocellar area and rest of head light (Fig. 1). Pronotum light brown with median yellow stripe and lateral, brown rugosities (Fig. 1). Wings hyaline, veins medium brown. Long ventral hair at posterior margin of each cercal segment. Median of each abdominal tergum with patch of long stout setae, mesoposterior margin of 9th tergum with patch of stout barrel-like spinulae

Plate XVIII, Figs. 1-4. *I. acula*. 1. adult head and pronotum (scale: 1 mm = .03 mm). 2. male vesicle and 8th sternum (1 mm = .03 mm). 3. male paraproct, lateral aspect (1 mm = .01 mm). 4. male terminal, abdominal terga (1 mm = .03 mm).



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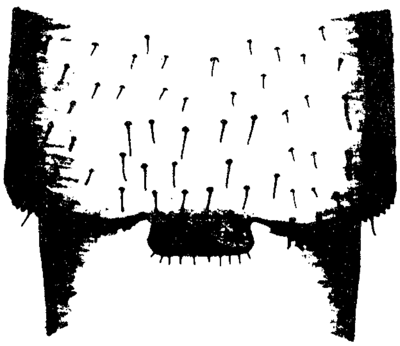

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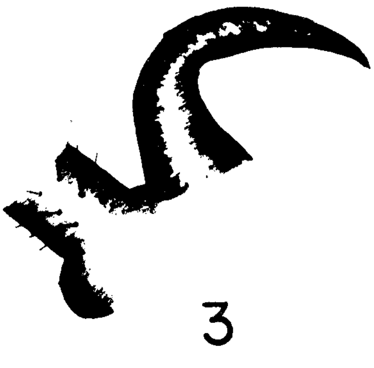

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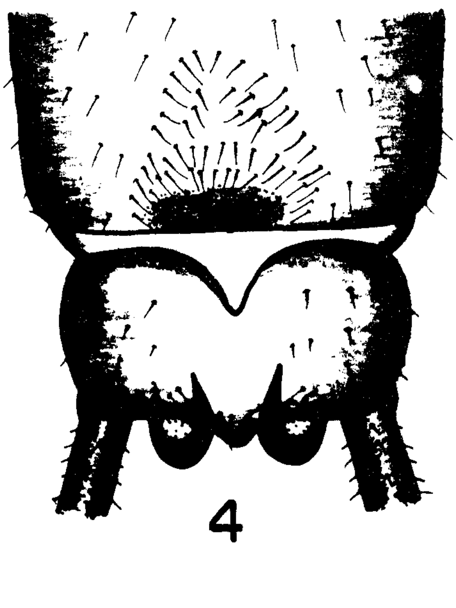

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and long fine hairs (Fig. 4). Paraprocts long, tapering to acute points apically, recurving over 1/4 10th tergum (Fig. 3). Vesicle rectangular, row of small fine hairs on apex, darker than rest of segment (Fig. 2). Mesal section of aedeagus bearing patch of concentrated, stout, golden brown spinulae (longitudinal, cylindrical sclerotized structure difficult to observe because of light pigmentation, Jewett, 1962).

Female.-- Unknown.

Nymph.-- Unknown.

Ova.-- Unknown.

Material examined.-- Paratypes, CALIFORNIA: Fresno Co., 7 mi. N.E. of Academy, elevation 800 feet, 19/V/1955, D. L. Abell, 2♂ (SJ).

Distribution.-- USA - CALIFORNIA (Fig. VIII).

Diagnosis and Discussion

I. acula is a very rare species, known only from 4 male specimens. Placement in this species group is questionable, and is based entirely on adult pigment patterns of the head and pronotum, and Jewett's (1962) description of the aedeagal sclerotized structure. The terminal portion of the abdomen had been cleared, and the aedeagus partially everted, in the 2 paratype specimens studied, although the aedeagal sac in both had apparently ruptured and the apical portion was missing, along with the sclerotized process. Discussion of relationships with other species must await association and description of nymphs, females, and ova. Nothing is known of the biology of this rare species.

Isoperla adunca Jewett

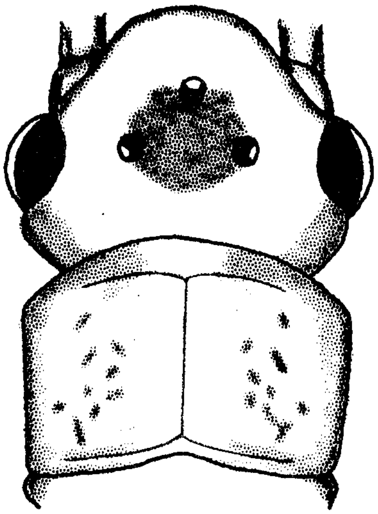
Isoperla adunca Jewett, 1962, 38:19. Holotype ♂, and allotype ♀; 5 mi. E. of Mt. Hamilton, Santa Clara Co., California, USA (CAS) (male and female genitalia, and aedeagl structure).

Isoperla adunca, Illies, 1966:393.

Description (Plates XIX and XX)

Male (Pl. XIX).-- Macropterous. Length of forewings 7-8 mm; length of body 7-9 mm. General body color medium brown. Interocellar area of head dark brown, forming solid, dark equilateral triangle between ocelli (Fig. 1). Pronotum light brown, with median light yellow stripe and small medium-brown rugosities (Fig. 1). Wings distinct, suffused with medium-brown pigment. Antennae and cerci dark brown, posterior margin of cercal segments with one long ventral hair. Paraprocts slender, deflected downward at apex, acute, recurving to level of 10th tergum (Fig. 3). Vesicle narrow at base, lateral margins parallel, apex rounded, with several medium-length hairs (Fig. 2). Aedeagus tubular, with short dorsal sclerotized clavate process, bifurcate at base (Fig. 4D); apex void of spinulae, anterodorsal margin

Plate XIX, Figs. 1-5. _I. adunca_. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. male vesicle and 8th sternum (1 mm = .03 mm). 3. male paraproct, lateral aspect (1 mm = .02 mm). 4. male aedeagus, lateral aspect, A. band of concentrated, small, fine spinulae, B. patch of short, stout spinulae and occasional long hair-like spinulae, C. patch of scattered long hair-like spinulae, D. sclerotized process (1 mm = .01 mm). 5. female subgenital plate (1 mm = .03 mm).



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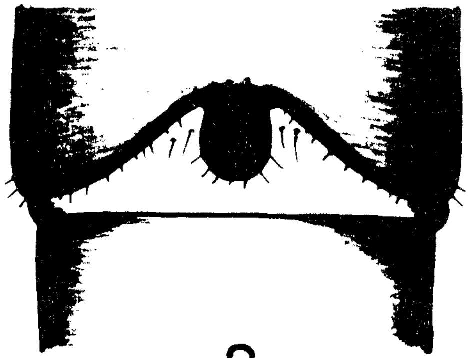

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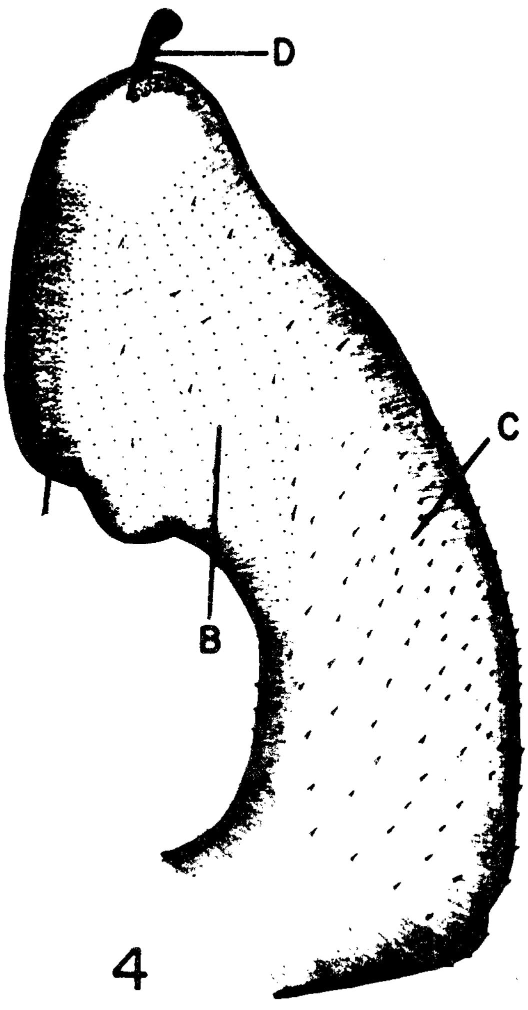

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bearing band of concentrated small, fine spinulae (Fig. 4A), posterodorsal margin and mesal section bearing short, stout spinulae and occasional long hair-like spinulae (Fig. 4B); pedicel bearing short, stout spinulae interspersed with long hair-like spinulae (Fig. 4C).

Female (Pl. XIX).-- Macropterous. Length of forewings 9-10 mm; length of body 8-10 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate slightly triangulate, rounded posteriorly with median emargination, produced 1/4 to 1/2 length of 9th sternum (Fig. 5).

Nymph.-- Unknown.

Ova (Pl. XX).-- General shape oblong, cross section triangular, except circular at poles (Fig. 5). Color yellowish brown. Length .33 mm; width .23 mm. Collar absent, chorionic ridges thin and elevated, forming lacy, hexagonal cell pattern; small, evenly spaced punctations within cells (Figs. 4-6); cells near bottom 1/3 elongate and triangular (Figs. 4-6). Micropyles small, scattered on ridges of triangular cells on one side (Fig. 7).

Material examined.-- TYPES: Holotype ♂, allotype p, CALIFORNIA, Santa Clara Co., 5 mi. E. of Mt. Hamilton, 31/V/1949, Collector ?, 1♂, 4♀ (CAS), 2♂, 1♀ (SGJ). Additional specimens - *USA* - CALIFORNIA: Alameda Co., 17 1/2 mi. S. of Livermore, Arroyo Macho, 27/VI/1965, P. H. Arnaud, Jr., 3♂, 6♀ (CAS).

Distribution.-- USA - California (Fig. VIII).

Diagnosis and Discussion

This species is similar to *I. denningi* (see diagnosis and discussion under *I. denningi*), although ova are more similar to *I. rainiera*.

This is a rare species restricted to the Coastal Range of California, and no studies on the life history or general biology have been done. It is found in creeks, and emergence occurs from May through Jun.

Isoperla bifurcata NEW SPECIES

Isoperla sordida, Gaufin et al., 1966, 14:71. In part (male and female genitalia, and sclerotized aedeagal process).

Isoperla sordida, Gaufin et al., 1972, 98:119. In part (male and female genitalia, and sclerotized aedeagal process).

Isoperla sordida, Baumann et al., 1977, 31:152. In part (male and female genitalia, and sclerotized aedeagal process).

Description (Plates XXI and XXIV)

Male (Pl. XXI).-- Macropterous. Length of forewings 6-9 mm; length of body 8-10 mm. General body color dark brown. Lateral ocelli of head with variable medium-brown band, usually not connected to anterior ocellus; interocellar space light; anterior ocellus with wide, medium-brown band and black, narrow, broadly "U"-shaped anterior band, wide, light brown band extending from front of compound eyes to base of antennae often connected to anterior ocellus; 2 dark brown spots anterior frons (Fig. 1). Pronotum mostly medium-brown, median light stripe, and rugosities dark brown (Fig. 1). Wings fumose, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Posterior margin of cercal segments with long ventral hair. Paraprocts short, stout, tapering slightly toward apex, bearing small, fine hairs, recurving forward to level of 10th tergum (Figs. 5 & 6). Vesicle truncate, lighter than rest of segment, bearing small, fine hairs, base with narrow, light band bearing small, fine hairs extending to lateral margins of segment (Fig. 3). Aedeagus capitate with posterodorsal lobe void of spinulae (Fig. 4D). Posterior sclerotized process bifurcate at base, projecting from posterior margin of lobe; dorsal arm forked at base-arm plate and at mid-length; arms of apical fork extending same length as base, pointed apically with sharp ventral spine (Fig. 4C & 7); small lobe bearing small, fine spinulae below insertion of sclerotized process (Fig. 4B), patch of small rounded spinulae on anterodorsal lobe (Fig. 4E); wide, dense band of small, stout spinulae covering mesal section (Fig. 4F), band of less dense, small, stout spinulae extending from mesal section to posterior margin (Fig. 4A).

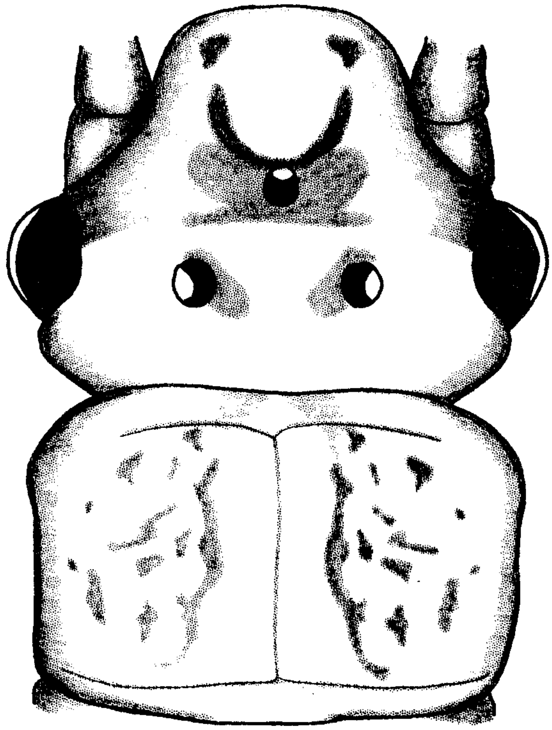
Female (Pl. XXI).-- Macropterous. Length of forewings 8-11 mm; length of body 10-12 mm. General body color and head-pronotal pigment pattern similar to male. Subgenital plate broad at base, shallow, concave, median apical emargination, produced approximately 1/4 length of 9th sternum, lateral margins of base with variable medium-brown spot (Fig. 2).

Nymph.-- Unknown.

Ova (Pl. XXIV).-- General shape oval, cross section circular (Fig. 1). Color medium-brown. Length .33 mm; width .25 mm. Collar absent; chorionic ridges elevated and thickened, forming irregularly shaped deep depressions, enclosing small punctations (difficult to observe due to depth of depressions) (Figs. 1-3). Micropyles set close together in pairs on top of ridges, near bottom 1/3 on one side (Fig. 4).

Material examined.-- TYPES: Holotype ♂, OREGON: Union Co., 6 mi. E. of Medical Springs, Lick Crk., 23/VII/1975, DFTM Project (deposited at USNM), allotype ♀, 6 mi. E. of Medical Springs, Lick Crk., 30/VI/1976, DFTM Project (deposited at USNM). Paratypes, OREGON: Union Co., 6 mi. E. of Medical Springs, Lick Crk., DFTM Project, 1/VII/1975, 1p, 9/VII/1975, 2♂, 2♀, 10/VII/1975, 1♀, 13/VII/1975, 3♂, 1♀, 14/VII/1975, 2♂, 3♀, 18/VII/1975, 25♂, 27♀, 22/VII/1975, 3♂, 3♀, 25/VII/1975, 2♂, 4♀, 28/VII/1975, 1♀, 29/VII/1975, 1/VIII/1975, 1♀, 5/VIII/1975, 1♀, 8/VIII/1975, 1♂,

Plate XXI, Figs. 1-7. I. bifurcata. 1. adult head and pronotum (scale: 1 mm = .03 mm). 2. female subgenital plate (1 mm = .06 mm). 3. male vesicle and 8th sternum (1 mm = .44 mm). 4. male aedeagus, lateral aspect, A. band of small, stout spinulae, B. small posterior lobe bearing scattered small, fine spinulae, C. sclerotized process, D. large dorsal lobe, E. patch of small rounded spinulae, F. concentrated band of small, stout spinulae (1 mm = .02 mm). 5. male paraprocts, lateral aspect (1 mm = .02 mm). 6. male paraprocts, dorsal aspect (1 mm = .02 mm). 7. aedeagal sclerotized process (1 mm = .03 mm).



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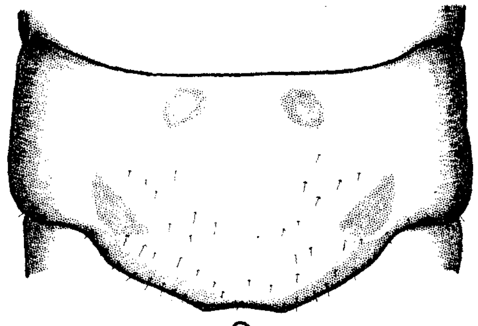

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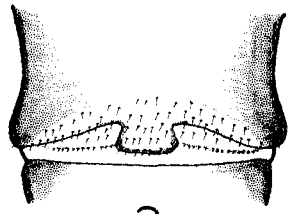

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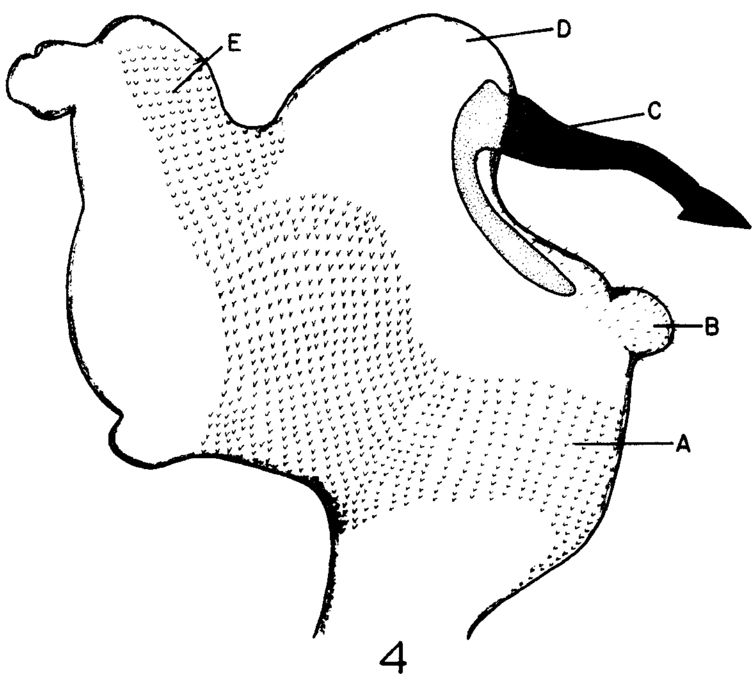

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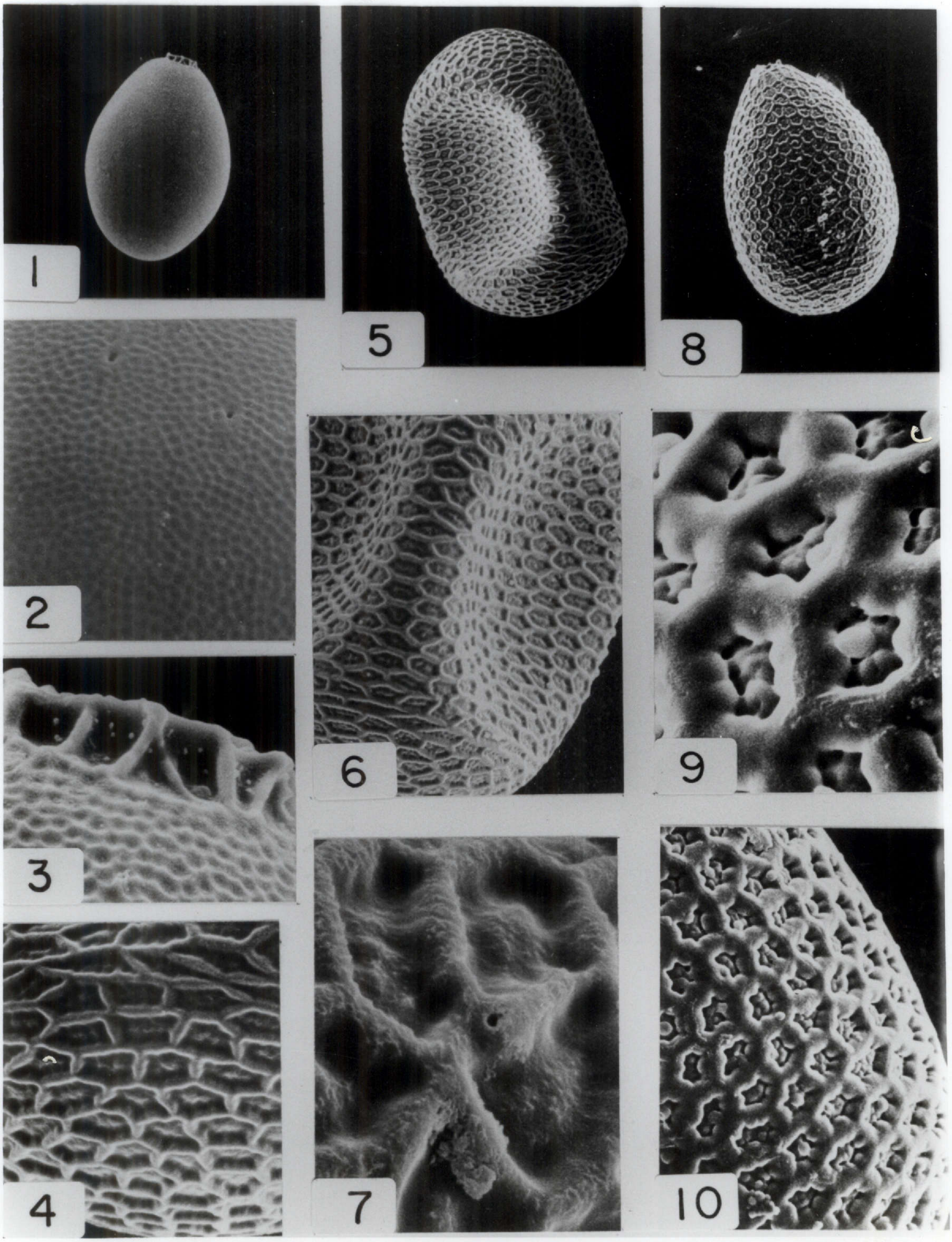
Plate XX. Scanning electron micrographs of *Isoperla* ova.*

Figs. 1-3. *I. denningi*. 1. whole ova 200X. 2. detail of chorion and micropyles 1000X. 3. detail of collar 2000X.

Figs. 4-7. *I. adunca*. 4. detail of chorion, polar area 700X. 5. whole ova 200X. 6. detail of chorion mesal section 400X. 7. detail of micropyle 3000X.

Figs. 8-10. *I. rainiera*. 8. whole ova 200X. 9. detail of chorion 2000X. 10. detail of chorion 700X.

* magnifications represent original values before reduction of plate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12/VIII/1975, 1♀, 30/VI/1976, 5♂, 15♀, 2/VII/1976, 2♂, 13/VII/1976, 3♂, 1♀, 16/VII/1976, 4♂, 3♀, 29/VII/1976, 1♀, 30/VII/1976, 1♂ (paratypes deposited at USNM, SWS, NTSU, CWS, RWB, and SJ). Additional specimens - USA - CALIFORNIA: Trinity Co., Carryville, ?/VI/1913, E. C. Van Dyke, 4♂, 2♀ (CAS). IDAHO: Blaine Co., Galena, Hwy. 93, Horse Crk., near junct. OREGON: Clackamas Co., Mt. Hood, Hood R. Meadows, 31/VII/1948, K. M. Fender, 2♂, 4♀ (LCMNH), Mt. Hood, Still Cr-., 15/VI/1947, S. G. Jewett, 1♂, 1♀ (LCMNH), Mt. Hood, Still Crk. Campground, 17/VI/1967, S. J. Jewett, 1♂, 1♀ (USNM), Swim, Still Crk., 15/VI/1947, S. G. Jewett, 1♂, 1♀ (LCMNH), Unknown Co., Olney, small crk., 8/VI/1940, S. G. Jewett, 3♂, 3♀ (UU). WASHINGTON: Pierce Co., Longmire, Mt. Rainier, 26/VII/1919, Fox, 1♀ (CAS).

Distribution.-- USA: California, Idaho, Oregon, and Washington (Fig. 8).

Diagnosis and Discussion

This species is most similar to *I. fusca*. Males can be distinguished by the truncate-shaped vesicle, stouter paraprocts, general spinulae pattern of the aedeagus, and aedeagal sclerotized process with shorter, stouter arms, not crossing and bearing a ventral spine at apex. Separation of females is difficult since the subgenital plate is very similar to *I. fusca* and *I. sordida*. In *I. sordida* the head pattern is much darker, with the interocellar area dark brown. The nymph of _I. bifurcata_ is unknown. Ova can be differentiated by the mudhc thicker, deeper chorionic ridges, irregularly shaped deep depressions, and absence of a collar.

Males and females from the type locality exhibited shorter wings than other populations examined, although body lengths were similar. In both males and females, the wings did not extend beyond the tip of the abdomen. The mean male and female wing lengths were 6.1 mm and 7.8 mm, respectively, compared to 9.1 mm and 10.0 mm from other populations. The head pattern of specimens from the type locality was also somewhat lighter than other populations, with no dark pigment band connecting the lateral ocelli to anterior ocellus; details of the male aedeagus and ova were identical in all populations.

This species has been confused with _I. sordida_. Gaufin et al. (1966) first illustrated the aedeagal sclerotized process under _I. sordida_, and this same illustration was repeated by Gaufin et al. (1972) and Baumann et al. (1977).

No studies on the life history or general biology have been done. Emergence extends from late Jun. to mid-Aug. in small creeks.

Etymology.-- This species name is derived from the double-forked nature of the aedeagus sclerotized process, dorsal arm.

Isoperla denningi Jewett

Isoperla denningi, Jewett, 1955, 13:150. Holotype ♂, and allotype ♀; 4 mi. W. of Tanbark Flat, Los Angeles Co., California, USA (CAS) (male and female genitalia, and aedeagal structure).

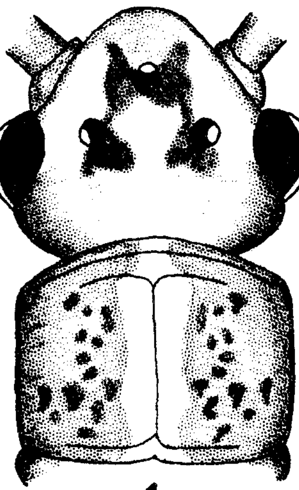
Isoperla denningi, Illies, 1966:400.

Additional references: Isoperla denningi, Jewett, 1960 (male and female genitalia, and aedeagal structure).

Description (Plates XX and XXII)

Male (Pl. XXII).-- Macropterous. Length of forewings 9-11 mm. Length of body 9-10 mm. General body color light brown. Ocelli of head connected by narrow, dark brown, inverted "W"-shaped band of pigmentation; interocellar space light yellow (Fig. 1). Pronotum light brown, with median yellow stripe and small, rounded, dark brown rugosities (Fig. 1). Wings hyaline, veins light brown. Posterior margin of cercal segments with a long ventral hair. Vesicle parallel-sided, slightly constricted at base, expanded apically, darker than rest of segment (Fig. 6). Paraprocts broad at base, tapering to points at apex, recurving forward to level of 10th tergum (Fig. 4). Aedeagus with expanded dorsal lobe bearing concentrated, small, stout spinulae (Fig. 5D), posterior margin with sclerotized process, bifurcate at apex with arms of fork short, rounded at tips, base of process bifurcate (Figs. 3 & 5C), one small

Plate XXII, Figs. 1-6. _I. denningi_. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. female subgenital plate (1 mm = .03 mm). 3. sclerotized aedeagal process, dorsal aspect (1 mm = .02 mm). 4. male paraproct, lateral aspect (1 mm = .02 mm). 5. male aedeagus, lateral aspect, A. large posteroventral lobe, B. small posterior, bearing small, fine spinulae, C. sclerotized process. D. expanded dorsal lobe (1 mm = .01 mm). 6. male vesicle and 8th sternum (1 mm = .03 mm).



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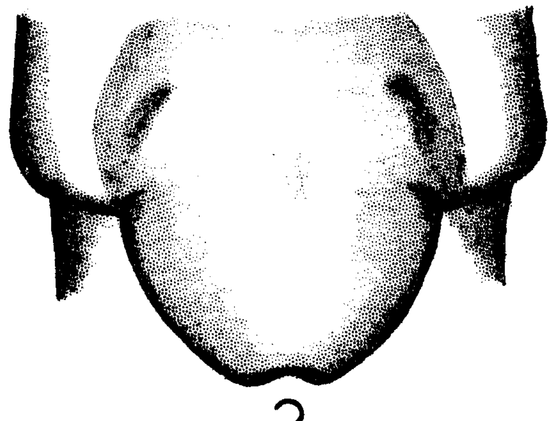

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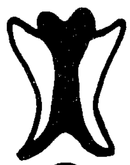

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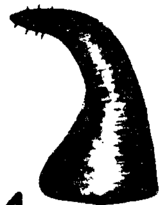

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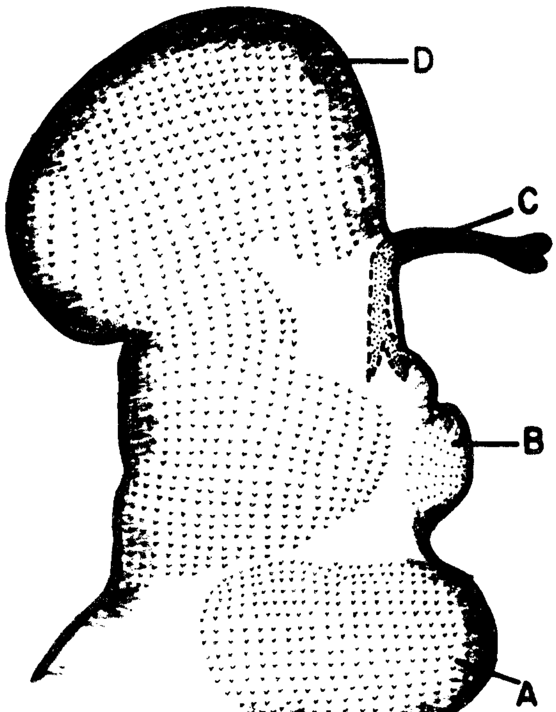

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lobe below base of process bearing patch of small, fine spinulae (Fig. 5B); one large posteroventral lobe covered with concentrated, small, stout spinulae (Fig. 5A).

Female (Pl. XXII).-- Macropterous. Length of forewings 11-13 mm; length of body 11-12 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, triangulate, median shallow emargination at apex, produced posteriorly over 1/2 9th sternum (Fig. 6).

Ova (Pl. XX).-- General shape oval, cross section circular (Fig. 1). Color light brown. Length .23 mm; width .17 mm. Collar slightly developed, with externally partitioned ridges (Figs. 1 & 3). Chorion covered with small, shallow, evenly spaced punctations, chorionic ridges absent (Figs. 1-3). Micropyles minute, arranged in pairs near bottom 1/3, on one side (Fig. 2).

Material examined.-- TYPES: Holotype ♂, and allotype ♀, CALIFORNIA, Los Angeles Co., 4 mi. W. of Tanbark Flat, 21/VI/1950, H. L. Hansen (CAS). Paratypes, CALIFORNIA: Los Angeles Co., 4 mi. W. of Tanbark Flat, 21/VI/1950, H. L. Hansen, 1♀ (CAS), Angels Camp, 22/V/1930, E. P. Van Cuzee, 2♀ (CAS); Tuolumne Co., Keystone, 25/IV/1951, J. S. MacSwain, 1♂, 1♀ (CAS); Trinity Co., Carrville, elevation 2,400-2,500 feet, 19/V/1934, E. C. Van Dyke, 1♀ (CAS). Additional specimens - CALIFORNIA: Los Angeles Co., Brent's Mt., 20/V/1939, Collector ?, 2♂, 1♀ (LCMNH); Riverside Co., 2 mi. W. of Riverside, 17/V/1955, Collector ?, 2♂, 1♀ (RWB), Idyllwild, 18/VI/1952, M. Cazier, W. Gertach, and R. Schrammel, 2♂, 1♀ (SJ); Tehama Co., Salt, 11/V/1954, H. P. Chandler, 1♀ (CAS); Tuolumne Co., Keystone, 25/IV/1951, J. S. MacSwain, 1♂ (SJ).

Distribution.-- USA: California (Fig. VIII).

Diagnosis and Discussion

This species is closely related to *I. adunca*. Males can be distinguished by the light interocellar area of the head, darker wings and body, paraprocts wider at base and not deflected downward at apex, large expanded dorsal lobe on aedeagus bearing small, stout spinulae, sclerotized aedeagal process bifurcate at apex, and lack of long,sharp hair-like spinulae on proximal aedeagal stalk. Females can be differentiated by the light interocellar area of the head, darker wings and body, and generally wider, more angulate subgenital plate (in some specimens the subgenital plate is very similar). Nymphs of both species are unknown. Ova can be separated by the smaller size, circular cross section, developed collar, and lack of elevated chorionic ridges and hexagonal-shaped cells.

This is apparently a rare species, and no biological studies have been made. Emergence begins in late Apr. and continues until the end of Jun. in creeks.

Isoperla fusca Needham and Claassen

Isoperla fusca Needham and Claassen, 1925, 2:146. Holotype

♂, and allotype ♀; Waterton Lakes, Alberta, Canada (CNM) (male and female genitalia, and aedeagus).

Isoperla fusca, Claassen, 1940, 232:200.

Isoperla fusca, Illies, 1966:403.

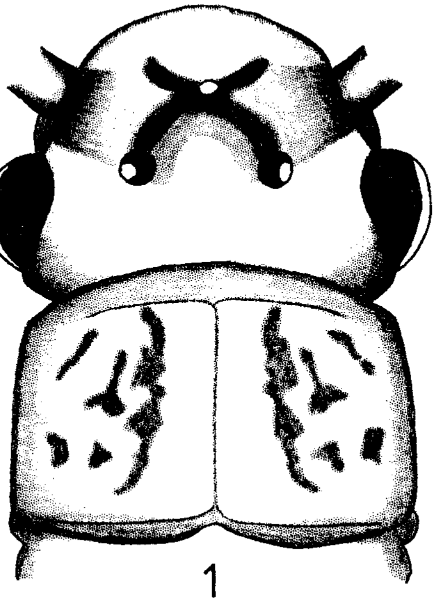
Isoperla fusca, Zwick, 1973:245.

Additional references: _Isoperla fusca_, Neave, 1929 (male aedeagus); Frison, 1942 (nymphal description, nymphal habitus, mandibles, maxillae, labrum, male and female genitalia, and adult head-pronotal pattern); Jewett, 1959 (male and female genitalia, and male aedeagus); Gaufin, 1964; Ricker, 1964; Knight et al., 1965 (ova); Gaufin et al., 1966 (male and female genitalia, and sclerotized aedeagal process); Newell, 1970; Gaufin et al., 1972 (male and female genitalia, and sclerotized aedeagal process); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia, and sclerotized aedeagal process).

Description (Plates XXIII and XXIV)

Male (Pl. XXIII).-- Macropterous. Length of forewings 7.5-8.6 mm; length of body 7.0-8.1 mm. General body color blackish brown. Ocelli of head connected by narrow, inverted, "U"-shaped band of black pigmentation; symmetrical, shallow "U"-band attached to inverted "U" at anterior ocellus; interocellar space light; wide, medium-brown band extending across head between bases of antennae (Fig. I). Pronotum

Plate XXIII, Figs. 1-8. _I. fusca_. 1. adult head and pronotum (scale: 1 mm = .04 mm). 2. nymph head, pro-, meso-, and metanota (1 mm = .06 mm). 3. male vesicle and 8th sternum (1 mm = .06 mm). 4. male paraproct, lateral aspect (1 mm = .02 mm). 5. sclerotized aedeagal process (1 mm = .03 mm). 6. nymph left hind leg (1 mm = .06 mm). 7. male aedeagus, lateral aspect, A. small posteroventral lobe, B. small mesoposterior lobe, C. sclerotized process, D. large conical anterodorsal lobe (1 mm = .04 mm). 8. female subgenital plate (1 mm = .03 mm).



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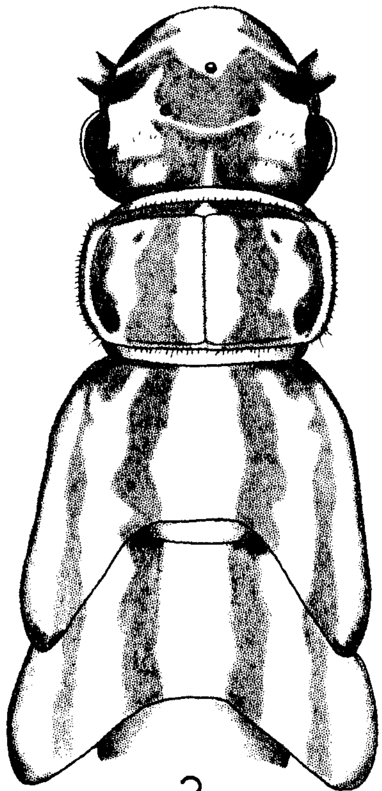

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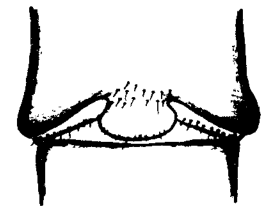

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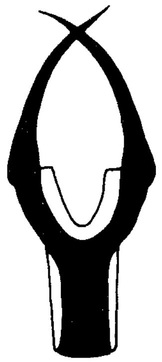

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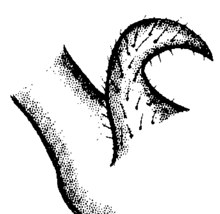

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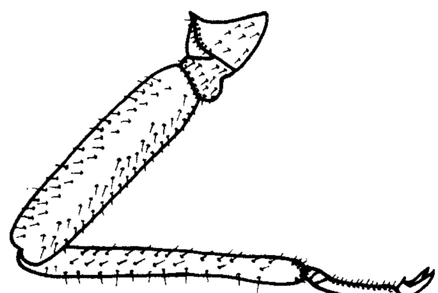

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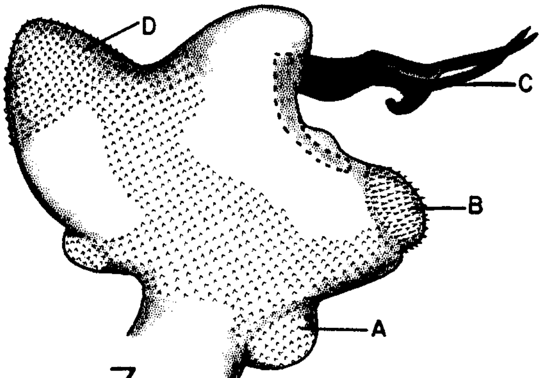

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medium-brown, with median light stripe, rugosities black (Fig. I). Wings hyaline, veins dark brown. Paraprocts short, tapering to points apically, covered with small, fine hairs, recurving anteriorly to level of 10th tergum (Fig. 4). Vesicle expanded at apex, evenly rounded posteriorly, lighter than rest of segment; few small, fine hairs at base (Fig. 3). Posterior margin of cercal segments with long ventral hair. Aedeagus with mesodorsal lobe void of spinulae, bearing posterior projecting sclerotized process, bifurcate at base; forked members of dorsal arm extending twice the length of base, tapering apically to long, fine points, crossed near apex; arms of forks bearing bent, finger-like ventral spine near 1/3 length (Fig. 7C); posterior lobe under projecting sclerotized process, covered with long, fine hair-like spinulae (Fig. 7B); small posteroventral lobe bearing small, stout spinulae (Fig. 7A); large, conical, anterodorsal lobe covered with small, stout spinulae (Fig. 7D); large patch of small, stout spinulae extending from anterodorsal lobe to posterior margin, rectangular patch void of spinulae below anterodorsal lobe.

Female (Pl. XXIII).-- Macropterous. Length of forewings 9.0-10.5 mm; length of body 9.0-11.0 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate broad at base, evenly rounded posteriorly, with shallow median emargination, produced approximately 1/4 length of 9th sternum (Fig. 8).

Nymph (Pl. XXIII).-- Length of mature male nymph 7.8-9.6 mm; length of mature female nymph 9.6-10.6 mm. Interocellar area of head dark brown, with lateral arms extending to bases of antennae; broad, bowl-shaped brown pigmentation extending backward from near lateral ocelli; epicranial arms and stem a fine, "Y"-shaped light band; variable dark spots behind eyes; occipital ridge with a few scattered, small, fine spinulae (Fig. 2). Pronotum with median light stripe and 4 longitudinal dark brown bands; margin fringed with small, stout setae, occasional long hairs interspersed at upper and lower angles (Fig. 2). Meso- and metanota with 4 dark brown longitudinal bands continuing from pronotal bands (Fig. 2). Outer surface of femora, tibiae and tarsi interspersed with spine-like setae, dorsal margins without typical fringe of long, fine hairs (Fig. 6). Abdominal terga with 3 longitudinal light stripes, one median and 2 lateral. Posterior margin of cercal segments with a whorl of small, stout setae.

Ova (Pl. XXIV).-- General shape oval (most appear crinkled due to alcohol preservation), cross section circular (Fig. 5). Color light brown. Length .30 mm; width .21 mm. Collar slightly developed (Fig. 5). Chorionic ridges elevated, forming hexagonal cells, each containing numerous, evenly spaced punctations (Figs. 5-7). Micro-

Plate XXIV. Scanning electron micrographs of *Isoperla* ova.*

Figs. 1-4 & 8. *I. tilasqua*. 1. whole ova 200X. 2. detail of chorion 400X. 3. detail of chorion 700X. 4. detail of micropyle 2000X. 8. detail of chorion at pole and 1000X.

Figs. 5-7. *I. fusca*. 5. whole ova 200X. 6. detail of chorion 400X. 7. detail of micropyle 1000X.

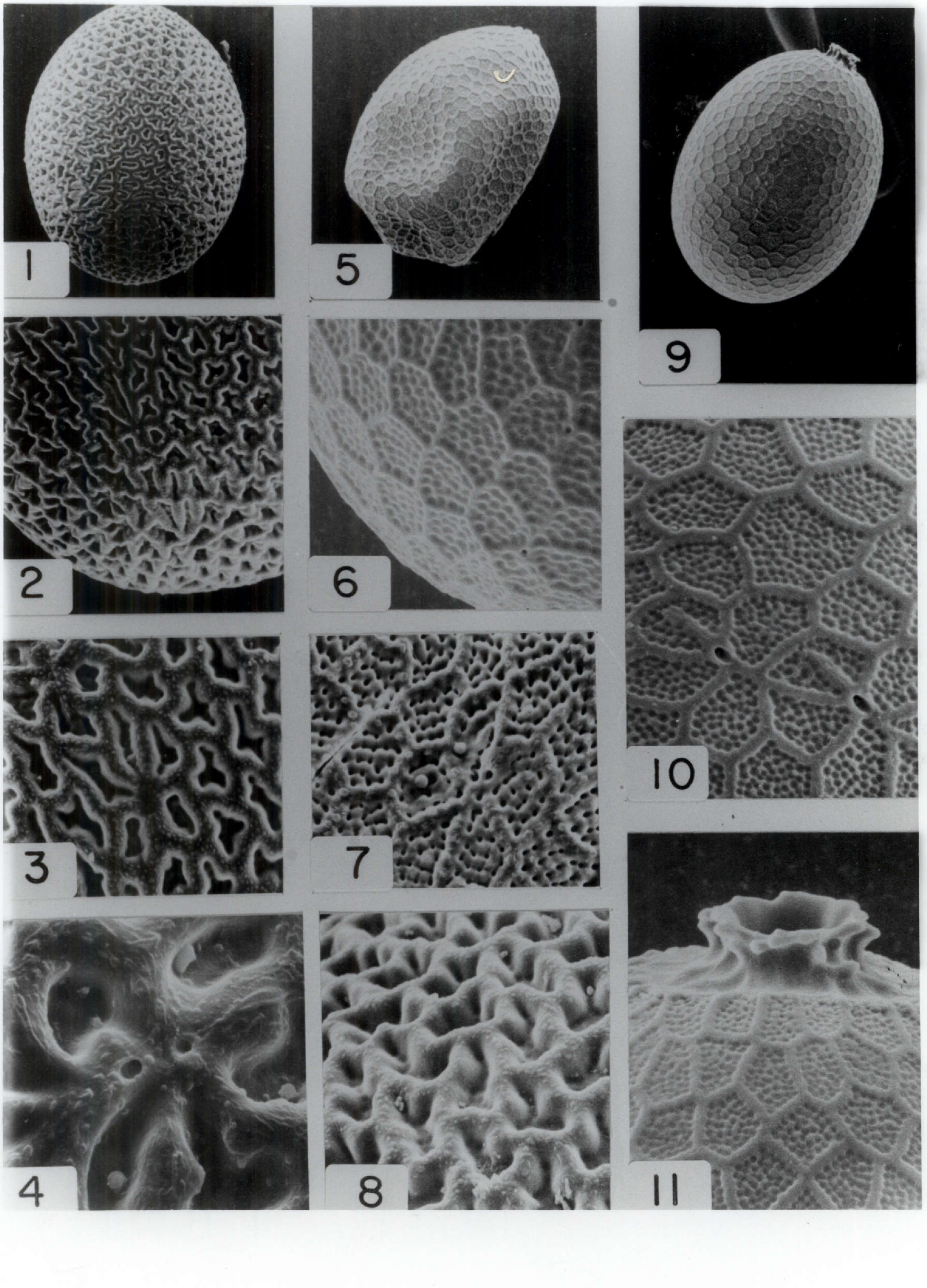
Figs. 9-11. *I. sordida*. 9. whole ova 200X. 10. detail of chorion and micropyles 1000X. 11. detail of collar 1000X.

* magnifications represent original values before reduction of plates

pyles minute, arranged singularly on top of ridges near bottom 1/3, on one side (Fig. 7).

Material examined.-- Paratypes; CANADA, Alberta, Waterton Lakes, 12/VII/1923, J. McDunnough, 2♂, 2♀ (CU #1,167). Additional specimens - CANADA: ALBERTA, Baniff National Park, Lake Louise Crk., Lake Louise, 27/VII/1968, A. R. Gaufin, 3♂, 3♀ (RWB), Waterton Lakes, Kootenair R., 1/VIII/1970, A. R. Gaufin, 1♂ (UU). USA - IDAHO: Fremont Co., S. fork of Fish Crk., N. of Warm R., 8/VII/1972, R. L. Newell, 1♂, 1♀ (RWB); Lemhi Co., crk. near Gibbonsville on Hwy. 93, 17/VI/1965, A. R. Gaufin, 1♂ (UU), Hwy. 93, S. of North Fork, Wagonhammer Springs, 17/VI/1965, A. R. Guafin, 1♂, 2♀ (RWB). MONTANA: Beaver Head Co., Polaris Wise R. Road, Gold Crk., 7/VIII/1966, J. R. Grierson, 1♂ (UU); Carbon Co., 16 mi. W. of Red Lodge, W. fork Rock Crk., 29/VII/1966, J. R. Grierson, 1♂ (UU); Flathead Co., Birch Lake, 28/VII/1967, P. Milam, 2♂, 2♀ (UU), Birch Crk., 16/VII/1970, A. R. Gaufin, 1♂ (UU), Birch Lake, 10/VIII/1967, P. Milam, 3♂, 9♀ (UU); Glacier Co., small crk. near Rising Sun Information Point, Glacier National Park, 6/VII/1962, A. R. Gaufin, 102 nymphs (UU), Glacier National Park, Iceburg Lake, Iceburg Crk., 30/VII/1965, A. V. Nebeker, 1 nymph (UU), Glacier National Park, Two Medicine Lake, 31/VII/1965, A. R. Gaufin, 2♀ (UU), Glacier National Park, Rising Sun Crk., at St. Mary's Lake, 23/VI/1965, A. V. Nebeker, 8 nymphs (UU), Glacier Park, Iceburg Crk., 27/VII/1965,

A. R. Gaufin, 4 nymphs (UU), Glacier Park, Belly R., 9/VII/1970, C. M. Yarmoloy, 1♂ (UU), Hwy. 89, Cutbank Crk., 22/VII/1966, A. R. Gaufin, 1♂ (UU), Glacier National Park, Trib. of Lake Mary, going to Rising Sun Observation Point, near ranger station, 6/VII/1967, A. R. Gaufin, 6♂ (RWB), small stream near Rising Sun Observation Point, 2/VII/1966, A. R. Gaufin, 3♂ (UU), 6/VII/1963, A. R. Gaufin, 3♂, 2♀ (UU), 6/VII/1962, A. R. Gaufin, 3♂, 1♀ (UU), 10/VII/1964, A. R. Gaufin, 8♂, 1♀ (UU), 9/VII/1964, A. R. Gaufin, 2♂ (UU), 29/VII/1970, A. R. Gaufin, 13♂, 15♀ (UU), 9/VII/1964, A. R. Gaufin, 1♂, 1♀ (UU), 18/VII/1965, A. R. Gaufin, 3♂, 2♀ (UU), near ranger station, Belly R., 3/VII/1970, C. M. Yarmoloy, 1♂ (UU), Glacier National Park, Fish Crk., 9/VII/1965, A. R. Gaufin, 3♂, 1♀ (UU), Glacier National Park, Trib. of Lake Mary, going to Rising Sun, near ranger station, 6/VII/1963, A. R. Gaufin, 3♂, 1♀ (RWB), Glacier National Park, Fish Crk. at junct. with McDonald Crk., 2/VII/1965, A. R. Gaufin and R. K. Allen, 2♂ (UU), Glacier National Park, Swift Current Lake, 17/VII/1965, A. R. Gaufin, 1♂ (UU), crk. 1/4 mi. N. of Bobb, 3/VII/1965, A. R. Gaufin, 2♂, 1♀ (RWB), Hwy. 2, Glacier Park, Tunnel Crk., 12/VII/1963, Collector ?, 2♂ (UU), Glacier National Park, Many Glover Campground, Webur Crk., 13/VII/1963, A. R. Gaufin, 1♂ (UU); Lake Co., Hwy. 32C, Lost Crk., 10/VII/1963, A. R. Gaufin, 3♂, 3♀ (UU); Meagher Co., Deeper, Sulpher Crk., 8/VII/1966, J. R. Grierson, 1♂ (UU);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Missoula Co., Camp Crk., 23/VI/1967, A. R. Gaufin, 5♂, 10♀ (UU), W. of Lake Alva, Uhler Crk., 20/VI/1969, R. L. Newell, 1♂ (UU), Sawyer Crk., 23/VI/1967, A. R. Gaufin, 1♂ (UU), 6 mi. above Miller Crk., Little Pork Crk., 20/VII/1965, J. R. Grierson, 1♂ (UU); Powell Co., Monture Crk. Rd., McCabe Crk., 11/VII/1970, A. R. Gaufin, 1♂ (UU); Ravali Co., 17 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 1♂ (UU), 2.6 mi. above Hwy. 93, Bear Crk., 12/VII/1965, J. R. Grierson, 1♂ (UU), 4.0 mi. above Black Bear ranger station, Daly Crk., 27/VII/1965, J. R. Grierson, 1♂, 1♀ (UU), 17 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 2♀ (UU), Hwy. 93 N. of Victor, Big Crk., 18/VI/1965, A. R. Gaufin, 1♀ (UU), Florence, 3/VII/1912, Collector ?, 1♂ (CU), 15 mi. above Hwy. 93, Lost Horse Crk., 30/VII/1965, J. R. Grierson, 1♀ (UU); County ?, W. of McGregor, McGregor Crk., 1/VII/1967, A. R. Gaufin, 1♂ (UU); County ?, Kiowa, Cutbank R. and Tribs., 12/VII/1959, S. G. Jewett, 3♂, 2♀ (USNM). WASHINGTON: Pend Oreille Co., elevation 3,150 feet, Thomas Lake, Little Pend Oreille Lakes, 19/VI/1954, B. Malkin, 1♂ (SJ). WYOMING: Park Co., Yellowstone National Park, Dunraven Pass, Mt. Washburn, 2/VIII/1940, T. H. Frison and T. H. Frison, Jr., 4♂, 1♀, 2 nymphs, 1 exuvia (INHS).

<u>Distribution</u>.-- CANADA: Alberta, British Columbia; USA: Idaho, Montana, Oregon, Washington, and Wyoming (Fig. VIII).

Diagnosis and Discussion

This species is closely related to I. bifurcata (see diagnosis and discussion under I. bifurcata), although ova characters are closer to I. sordida.

There is no detailed knowledge of the biology. Material examined was collected mid-Jun. to mid-Aug., and was most abundant in mid-Jul. Adults and nymphs were collected from small rivers and creeks.

Isoperla petersoni Needham and Christenson

Isoperla petersoni Needham and Christenson, 1927, 201.
    Type locality - Peterson's Spring, head of Logan R., Cache Co., Utah, USA (no type designation, habitus, adult male and nymph).

Isoperla fontium Neave, 1929, 4:161. Holotype ♂, and allotype p, Maligne Lake, Alberta, CANADA (CNM) (nymphal mandible, maxillae, male and female genitalia, and sclerotized aedeagal process). Syn. Ricker, 1954.

Isoperla petersoni, Needham (in Claassen), 1937, 69:81 designation of holotype P, and allotype p, Peterson's Spring, head of Logan R., Cache Co., Utah, USA (Cu #1,687) (male and female genitalia, aedeagus, and adult head-pronotal pattern).

Isoperla fontium, Claassen, 1940, 232:200.

Isoperla petersoni, Claassen, 1940, 232:204.

Isoperla petersoni, Ricker, 1954, 51:39. Syn. indicated.

Isoperla petersoni, Illies, 1966:415.

Isoperla petersoni, Zwick, 1973:250.

Additional references: *Isoperla petersoni*, Claassen, 1931 (nymphal habitus); Knowlton and Harmston, 1938; Jewett, 1959 (male genitalia and aedeagus); Ricker, 1964; Gaufin, 1964; Knight et al., 1965b (ova); Gaufin et al., 1966 (male and female genitalia, and sclerotized aedeagal process); Nebeker and Gaufin, 1966; Baumann, 1971; Gaufin et al., 1972 (male and female genitalia, and sclerotized aedeagal process); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia, and sclerotized aedeagal process). *I. fontium*, Ricker, 1943 (adult head-pronotal pattern), 1944.

Description (Plates XXIV and XXV)

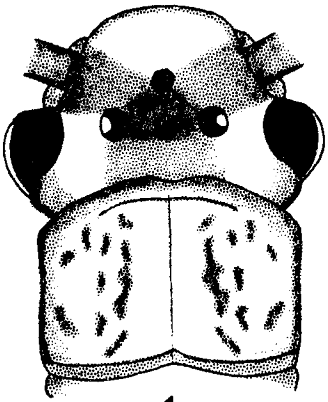
Male (Pl. XXV).-- Macropterous-brachypterous. Length of forewings (macropterous) 9.0-10.5 mm; length of body 8.0-12.5 mm; length of forewings (brachypterous) 1.4-2.0 mm, length of body 7.5-9.5 mm. General body color dark brown. Interocellar area of head dark brown, forming equilateral triangle between ocelli; broad, diffuse brown "Y"-shaped band enclosing equilateral triangle and extending from base of antennae to occiput (Fig. I). Pronotum medium brown, median light stripe, rugosities dark brown (Fig. I). Wings fumose, veins dark brown. Long ventral hair at posterior margin of cercal segments. "C"-

shaped paraprocts (laterally) stout, tapering slightly toward apex, apex blunt, distinctively deflected downward to a point, recurving anteriorly to level of 10th tergum, dorsal surface bearing small fine hairs; anterior tooth near base (Fig. 2). Vesicle constricted at base, posterior margin rounded, few small fine hairs at base, slightly lighter than rest of segment (Fig. 5). Aedeagus with mesodorsal conical-shaped lobe void of spinulae, bearing posterior projecting sclerotized process, bifurcate at base; dorsal arm developed into single long, curved, tapered, striolate, needle-like rod (Fig. 4C), patch of long, hair-like spinulae under process, continuing as narrow band down posterior margin (Fig. 4A); anterodorsal portion with rounded lobe bearing concentrated dorsal patch of large, stout spinulae (Fig. 4D); constricted area and posterior 1/2 of anteroventral lobe with dense band of small, stout spinulae (Fig. 4B).

Female (Pl. XXV).-- Macropterous-brachypterous. Length of forewings (macropterous) 11-15 mm, length of body 10-15 mm; length of forewings (brachypterous 3.0-5.5 mm, length of body 8-13 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate evenly rounded posteriorly, with wide, shallow median emargination, produced 1/4 length of 9th sternum, long, stout hairs interspersed near base (Fig. 6).

Nymph (Reared) (Pl. XXV).-- Length of mature nymphs

Plate XXV, Figs. 1-6. _I_. _petersoni_. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. male paraproct, lateral aspect (1 mm = .02 mm). 3. nymph head and pronotum (1 mm = .06 mm). 4. male aedeagus, lateral aspect, A. patch of long, hair-like spinulae, B. concentrated band of small, stout spinulae, C. sclerotized process, D. anterodorsal lobe (1 mm = .03mm). 5. male vesicle and 8th sternum (1 mm = .03 mm). 6. female subgenital plate (1 mm = .03 mm).



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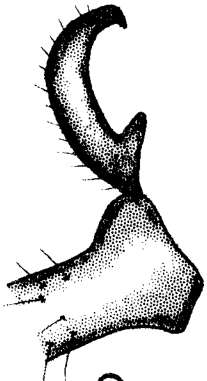

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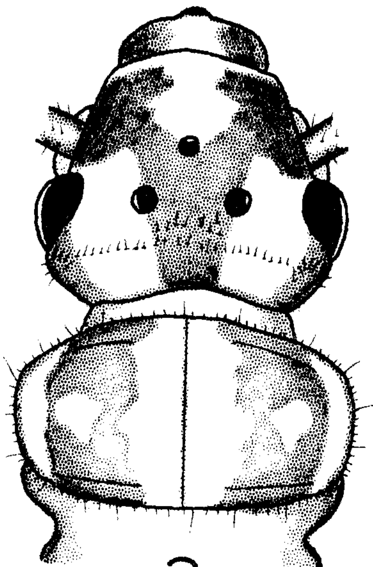

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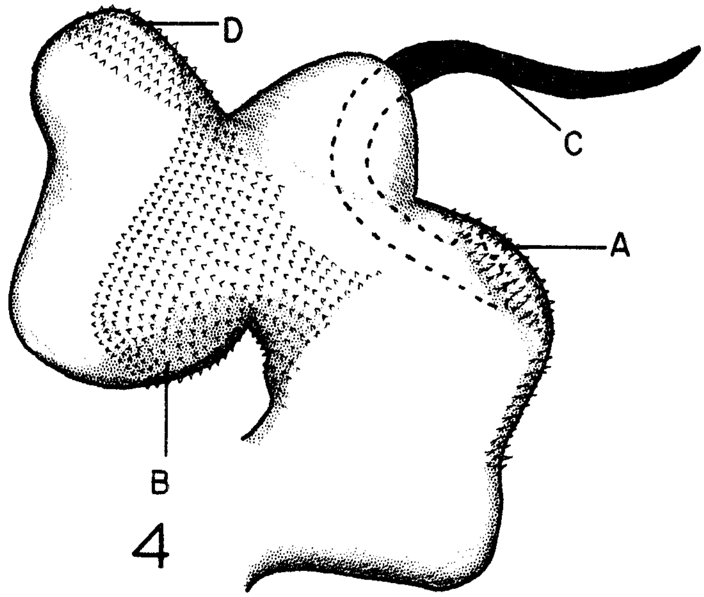

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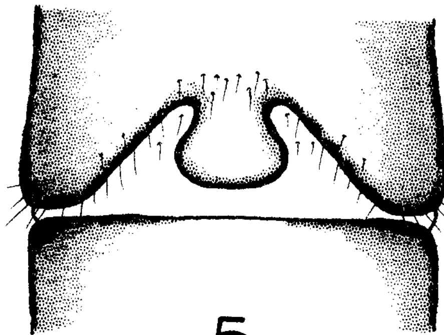

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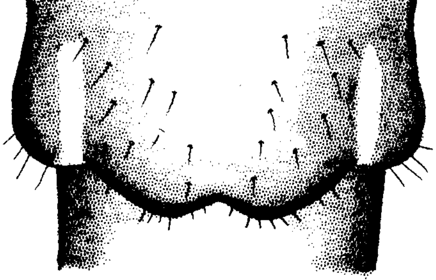

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9-12 mm. General body color medium brown. Dorsum of head with distinct medium brown band extending from occiput, covering interocellar area, and with lateral expanding arms extending to bases of antennae and forward, to near anterior margin of frons; light "U"-shaped area anterior to median ocellus, and 2 rectangular light areas mesad of eyes; occipital ridge bearing row of small, stout spinulae (Fig. 3). Pronotum light brown, median yellow stripe, 2 wide lateral brown bands, each enclosing light spot, rugosities absent; bordered by light margins; pronotum fringed with small, stout hairs and scattered longer hairs (Fig. 3). Femora, tibiae, and tarsi with scattered dorsal fringe of long, fine hairs, long, stout, spine-like setae interspersed on outer surface of femur, tibiae with row of medium-length stout, spine-like setae below dorsal fringe and at ventral margin. Abdominal terga with 3 light longitudinal stripes, one mesal and 2 lateral. Posterior margin of cercal segments with whorl of small, stout setae.

Ova (Pl. XXIV).-- General shape oval, cross section circular (Fig. 9). Color light brown. Length .29 mm; width .22 mm. Collar well developed, crown-shaped, sparse outer partitions ridges (Figs. 9 & 11). Chorionic ridges narrow, elevated, forming distinct hexagonal-shaped cells, each enclosing numerous, evenly spaced punctations (Figs. 9-11). Micropyles arranged in row of 2-5 on distinct, elevated, thickened transverse polar ridge near bottom 1/3, on one side (Fig. 10).

Material examined.-- TYPES: I. petersoni, holotype ♂, and allotype p, USA - UTAH: Cache Co., Logan R., 17/VI/1926, J. G. Needham (CU #1,689). Paratypes, UTAH: Cache Co., Logan R., 26/VII/1926, J. G. Needham, 5♂, 1♀, 4 exuviae, 3 nymphs (CU #1,689). I. fontium, Paratypes, CANADA - ALBERTA: Maligne Lake, Date ?, Collector ?, 3♂, 2♀ (CU #1,168). Additional specimens - CANADA: ALBERTA, Forty Mile Crk., 19/VIII/1969, C. M. Yarmoloy, 7♂, 2♀ (UU), between Bow Falls and Spray R. junct., 18/VIII/1969, C. M. Yarmoloy, 6♂, 2♀ (UU & BS), above Bow Falls and Bow R., 19/VIII/1969, C. M. Yarmoloy, 3♂, 2♀ (UU), Baniff, Marradine Lake, 18/VIII/1969, C. M. Yarmoloy, 8♂, 4♀ (RWB), Baniff, above Bow Falls, 19/VIII/1969, C. M. Yarmoloy, 13♂, 4♀ (RWB). BRITISH COLUMBIA, Glacier National Park, below Fay Rock, 3/VIII/1961, J. Ricker, 1♂, 1♀ (WR), Glacier National Park, Incomappleux R. system, Freeze Crk., J. Ricker, 1♂, 1♀ (WR), Seekirks Mts., near Tangier Pass, 17/VIII/1961, J. Ricker, 1♂ (WR). SASKATCHEWAN, Hanson Lake Rd., stream entering Bow R., 21/VI/1974, L. Dodsall, 1♀ (US). USA - ALASKA: Anchorage jeep trap, Granite Crk., 8/IX/1966, K. N. Sommerman, 1♂ (USNM), Alaska N. Slope, Echooko R. Springs, 23/VII/1971, P. McCart, 4♂, 16♀ (WR). IDAHO: Fremont Co., Head Warm R., 19/VI/1955, S. G. Jewett, 13♂, 17♀ (SGJ). MONTANA: Gallatin Co., Hwy. 191, bridge near Baconrind, W. Gallatin R., 26/VII/1963, A. R. Gaufin, 1♂ (UU); Glacier Co., Glacier National Park, Red Ruck Falls, 28/VII/1970, A. R. Gaufin, 10♂, 15♀ (UU). UTAH: Cache Co., Logan Canyon, Rick's Spring, 22/IX/1963, G. F. Knowlton, 13♂, 2♀ (UU), Logan Canyon, Rick's Spring, 29/VIII/1964, A. V. Nebeker, 7♂, 2♀, 9 exuviae (RWB), Logan Canyon, 24/IX/1939, W. P. Nye, 4♂, 2♀ (INHS), Logan Canyon, 29/X/1959, G. F. Knowlton, 1♂ (RWB), Logan Canyon, 21/IX/1961, G. F. Knowlton, 9♂ (BS), Logan Canyon, Utah Scout Camp, 17/IV/1938, D. E. Hardy, 18♂, 2♀ (RWB & INHS), Logan Canyon, Spring Hollow Crk., 9/XI/1963, A. V. Nebeker, 14♂, 3♀ (UU); Wasatch Co., Hwy. 40, above Strawberry Res., Trout Crk., Stat. 1, 23/VIII/1966, D. C. Hales, 3♂, 2♀ (RWB), 27/VII/1966, 1♀ (RWB), 6/VII/1966, 1♀ (RWB), 13/VIII/1966, 3♂, 2♀ (RWB), 15/IX/1964, 2♂, 4♀, 1 exuvia (RWB), 4/XI/1965, 1♂, 2♀ (UU), Stat. 2, 18/V/1965, 3 nymphs (UU), 20/VI/1965, 25 nymphs (UU), 7/VI/1965, 22 nymphs (UU), 8/VIII/1965, 16 nymphs (UU), 18/V/1965, 22 nymphs (UU), 12/I/1966, 24 nymphs (UU), 4/X/1966, 4 nymphs (UU), 6/VIII/1966, w nymphs (UU), 8/IX/1965, 2 nymphs (UU), 7/VI/1965, 4 nymphs (UU), 28/XII/1965, 3 nymphs (UU), 24/IV/1966, 15 nymphs (UU), 15/VI/1965, 3 nymphs (UU), 15/IX/1966, 1 nymph (UU), 20/VI/1965, 15 nymphs (UU), 13/VII/1966, 3 nymphs (UU), 18/III/1966, 25 nymphs (UU), 13/VII/1966, 7 nymphs (UU), 8/VIII/1965, 5 nymphs (UU), 4/X/1966, 7 nymphs (UU), 13/VII/1966, 5 nymphs (UU), 18/V/1965, 8 nymphs (UU), 14/V/1966, 27 nymphs (UU), 6/VIII/1966, 23 nymphs (UU), 20/VI/1965, 14 nymphs (UU), 7/VII/1965, 18 nymphs (UU), 23/VIII/1966, 12 nymphs (UU), 18/III/1966, 25 nymphs (UU), 3/IV/1965, 6 nymphs (UU). WYOMING: Teton Co., Grant Teton National Park, Cascade Canyon, 9/VIII/1940, T. H. Frison, 15♂ (INHS), Wilson, Coal Crk., 12/VIII/1940, T. H. Frison, 2 nymphs (INHS).

Distribution.-- CANADA: Alberta, British Columbia; USA: Alaska, Idaho, Montana, Utah, and Wyoming (Fig. VIII).

Diagnosis and Discussion

This species is similar to *I. fusca*. Males can be distinguished by the completely dark interocellar area of the head, apex of paraprocts deflected downward and blunt at tips, and single, curved, needle-like sclerotized process of the aedeagus. Females can be differentiated by the completely dark interocellar area of the head, and narrower subgenital plate with scattered, stout setae (subgenital plates of *I. sordida*, *I. fusca*, and *I. petersoni* are very similar, and each species exhibits some variations in shape and presence or absence of a median emargination, making separation difficult at times). Nymphs can be separated by the continuous row of small, stout setae on occipital ridge, absence of 4 longitudinal dark bands on meso- and metanota, and presence of a scattered dorsal fringe of long, fine hairs on femora, tibiae, and tarsi. Ova can be distinguished by the presence of a well-developed collar and elevated, transverse micropyle ridge.

Authorship of this species has been confusing since its inception. Needham and Christenson (1927) reported that a new species had been collected from Peterson's Spring, Utah, and provided illustrations of the adult male and nymph, but no formal description or type designation was given. They indicated that the species had been described by Claassen under the name _Isoperla petersoni_. Claassen (1931) described the nymph, and Needham, in Claassen (1937), provided a detailed description of male and female genitalia, including the sclerotized process of the aedeagus, and also designated the male holotype and allotype, and 21 male, 5 female, and many exuvial and nymphal paratypes from the Logan River, Utah. Authorship of this species has been assigned to Claassen (Claassen 1931), and to Needham (Claassen 1937), but in accordance with the International Code of Zoological Nomenclature, Needham and Christenson's mention of the species must be considered under the section "indications" of the Code, and they must therefore retain authorship as indicated by Ricker (1954).

I. petersoni exhibits varying degrees of wing length in both males and females. Populations in southern latitudes appear to have much shorter wings and slightly smaller bodies than those of more northern populations. A general increase in wing length was noted from Utah to British Columbia (Table 1). One population from Alaska

Table I. Varying wing lengths of *I. petersoni*

	♂		♀	
	$\bar{X}$ wing length mm / range mm	$\bar{X}$ body length mm / range mm	$\bar{X}$ wing length mm / range mm	$\bar{X}$ body length mm / range mm
Utah, Cache Co., Logan R.	1.6 / 1.5-1.9	8.1 / 7.2-8.7	3.1 / 2.7-3.3	9.0 / 8.3-9.2
Utah, Wasatch Co., Trout Crk.	1.7 / 1.4-2.0	8.3 / 7.7-9.3	4.1 / 2.9-5.4	11.5 / 9.4-12.6
Wyoming Teton Co., Grand Teton Nat'l Park	5.2 / 4.5-5.8	9.1 / 8.4-10.1	10.0 / 9.1-11.1	10.1 / 9.6-11.8
Idaho, Fremont W., Head of Warm R.	9.3 / 8.8-9.9	9.1 / 7.9-9.8	11.5 / 10.6-12.5	10.7 / 9.5-11.1
Montana, Glacier Co., Red Ruck Falls	10.5 / 9.1-11.1	9.8 / 9.4-10.8	12.2 / 10.7-13.0	10.8 / 10.4-12.6
Alaska Echooka Springs	8.4 / 7.9-9.6	8.7 / 8.2-9.1	10.2 / 9.3-11.0	10.2 / 9.8-11.0
CANADA, Alberta, between Bow Falls and Spray R.	11.1 / 10.1-11.7	9.9 / 8.6-10.7	13.4 / 12.0-14.3	11.8 / 10.0-13.5
CANADA, British Columbia, Alberta Snowfield	11.6 / 10.8-12.3	10.8 / 9.8-12.6	14.7 / 14.2-15.0	13.4 / 11.4-14.6

exhibited shorter wings than other typically northern populations, but the specimens were collected from a spring, as were the Utah populations. It is thought that the more constant temperature regimes, characteristic of springs, probably alters wing length and nymphal development.

Needham and Christenson (1927) reported that adults were collected on moss-covered stones near the water's edge, and that eggs were found suspended in gelatinous masses from stones in the water.

No life history or general biology studies have been done for this species. Based on the material examined, emergence occurs mid-Jun. to late Oct., and the spcies occurs in springs and small creeks.

Isoperla rainiera Jewett

Isoperla rainiera Jewett, 1954a, 11:549. Holotype ♂, Mount Ranier National Park, Pierce Co., Washington, USA (CWS) (male vesicle and aedeagal sclerotized process).

Isoperla rainiera, Jewett, 1962, 38:19. Allotype ♀, Trib. of Salmon R., Mt. Hood, Clackamas Co., Oregon, USA (CAS) (female genitalia).

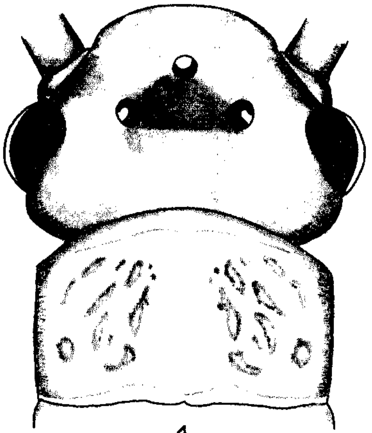
Isoperla rainiera, Illies, 1966:417.

Additional references: *Isoperla rainiera*, Jewett, 1960 (aedeagal sclerotized process).

Description (Plates XX and XXVI)

Male (Pl. XXVI).-- Macropterous. Length of forewings 8.5-9.0 mm; length of body 8.0-9.0 mm. General body color dark brown. Interocellar area of head completely dark brown, forming equilateral triangle between ocelli, diffuse, medium brown broad, "T"-shaped pigment band connecting bases of antennae and mesoposterior margin of head, enclosing ocellar triangle; two large light yellow spots between compound eyes (Fig. 1). Pronotum medium brown, light yellow median stripe, and numerous dark brown rugosities (Fig. 1). Dorsum of meso- and metathorax very dark. Antennae and legs dark brown, cerci light with long ventral hair at posterior margin. Wings fumose, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal and 3 each laterally. Vesicle constricted at base, expanded at apex, evenly rounded at posterior margin, with few small, fine hairs (Fig. 4). Paraprocts wide at base, tapering to sharp, fine points apically, dorsoposterior surface bearing small, fine hairs; curved forward to level of 10th tergum (Figs. 6 & 7). Aedeagus tubular, posterodorsal sclerotized process with short bifurcate base, apex of dorsal arm expanded, evenly rounded, with 2 sharp, lateral downward deflecting spines (Figs. 5 & 9D); band of scattered, small, fine, hair-like spinulae on dorsal surface (Fig. 9F); large apical lobe, anteroventral margin with smaller lobe void of spinulae

Plate XXVI, Figs. 1-10. *I. rainiera*. 1. adult head and pronotum (scale: 1 mm = .06 mm). 2. nymphal thoracic sterna (1 mm = .08 mm). 3. nymph head and pronotum (1 mm = .07 mm). 4. male vesicle and 8th sternum (1 mm = .05 mm). 5. aedeagal sclerotized process (1 mm = .03 mm). 6. male paraproct, dorsal aspect (1 mm = .08 mm). 7. male paraproct, lateral aspect (1 mm = .09 mm). 9. male aedeagus, lateral aspect, A. mesal band of small, rounded spinulae, B. anteroventral lobe, C. wide band of small, stout spinulae, D. sclerotized process, E. small mesodorsal lobe, F. scattered band of small, fine, hair-like spinulae (1 mm = .03 mm). 10. nymphal left hind leg (1 mm = .09 mm).



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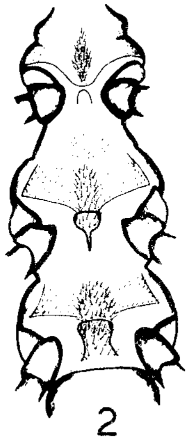

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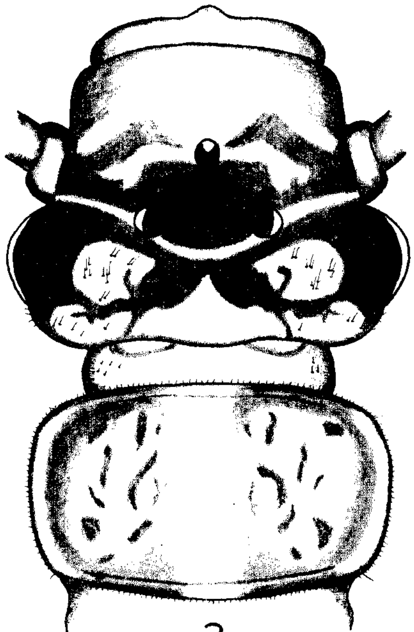

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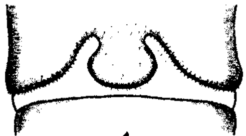

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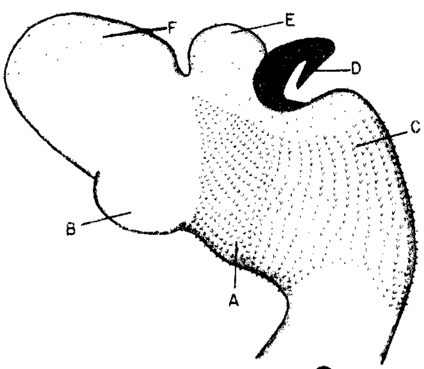

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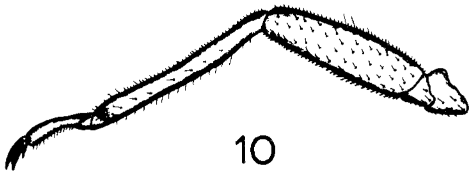

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(Fig. 9B), small mesodorsal lobe anterior to sclerotized process bearing small, fine, hair-like spinulae (Fig. 9E); mesal section with band of small, rounded spinulae (Fig. 9A), and band of small, stout spinulae extending from posterior margin to mesal section (Fig. 9C).

Female (Pl. XXVI).-- Macropterous. Length of forewings 9.4-10.4 mm; length of body 9.0-10.9 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate wide at base, evenly rounded posteriorly, produced approximately 1/4 length of 9th sternum (Fig. 8).

Nymph (Reared) (Pl. XXVI).-- Length of mature male nymph 9.5-10.5 mm; length of mature female nymph 10.0-11.4 mm. Interocellar area of head dark brown, 2 light yellow areas inside and behind each compound eye, with scattered, long, fine hairs; posterior margin of head mostly light yellow, head pattern of numerous narrow black pigment bands (Fig. 3). Pronotum medium brown, broad median light yellow stripe, lateral rugosities dark brown; margin fringed with small, stout hairs, occasional long hairs at upper and lower angles (Fig. 3). Femora, tibiae, and tarsi without typical dorsal fringe of long, fine hairs, outer surfaces with scattered, long, spine-like setae (Fig. 10). Pro-, meso-, and metathoracic sterna with median patch of long, golden brown setae, metasternal patch broadest (Fig. 2). Ventrum of abdomen cream yellow, dorsum mostly dark brown, with light, narrow median stripe. Cercal segments with whorl of short, stout hairs, and one long ventral hair at posterior margin.

Ova (Pl. XX).-- General shape oval, cross section circular (Fig. 8). Color medium brown. Length .30 mm; width .20 mm. Collar poorly developed (Fig. 8). Chorionic ridges elevated, thickened, forming obscured hexagonal-shaped depressions, with a number of small punctations (Figs. 8-10). Micropyles were not observed.

Material examined.-- TYPES: Allotype ♀, USA: OREGON, Clackamas Co., Mt. Hood, Trib. of Salmon R., 14/VII/1956, S. G. Jewett (CAS). Additional specimens - USA - OREGON: Clackamas Co., Mt. Hood, Trib. of Salmon R., 9/VII/1955, 1♀, 38 nymphs (SJ), Mt. Hood, Trib. of Salmon R., 24/VI/1956, S. G. Jewett, 1♂, 1♀ (SGJ), Mt. Hood, Trib. of Salmon R., 9/VII/1955, S. G. Jewett, 1♂ (RWB), Mt. Hood, Trib. of Salmon R., 23/VII/1955, S. G. Jewett, 2♂ (CAS), Mt. Hood, first crk. down from Timberline Lodge, on road to lodge, 31/V/1977, S. W. Szczytko and K. W. Stewart, 2♂, 5♀, 11 nymphs, and 1 exuvia (SWS & NTSU).

Distribution.-- USA - Oregon and Washington (Fig. VIII).

Diagnosis and Discussion

This species is similar to *I. sordida*. Males can be distinguished by the pedicellate vesicle, shorter, stouter, paraprocts, general shape and smaller size of the aedeagal sclerotized process, and presence of small, rounded spinulae on mesal section of aedeagus. Females can be differentiated by the general darker body color and the slightly longer, more evenly rounded subgenital plate. The nymph of *I. sordida* is unknown, but *I. rainiera* nymphs can be separated from all other known species within the group by presence of the long, golden brown setae on the pro-, meso-, and metathoracic sterna, and the intricate dark head pattern. Ova can be distinguished by the poorly developed collar, thickened, elevated chorionic ridges forming hexagnoal depressions, and lack of a micropyle ridge.

Nymphs of this species were successfully collected and reared from a small stream on Mt. Hood, Oregon. Nymphs were placed in styrofoam six-pac rearing chambers containing stream water, placed on ice and transported to Salt Lake City, Utah, via a commerical airlines flight. The rearing chambers were kept on ice while transported for 2 days by truck to Denton, Texas, and then maintained in an environmental chamber set at 8^{0} C (approximating stream temperature). Adults began to emerge after one week in the environmental chamber. Two males and 5 females were reared, and remained alive for approximately one week.

No life history or general biology studies have been made for this species. Based on the material examined, emergence occurs early Jun. to mid-Jul. The species is apparently restricted to small, high mountain streams.

Isoperla sordida Banks

Isoperla sordida, Banks, 1906a, 38:337. Holotype ♂; Los Angeles Co., California, USA (MCZ #11,338) (male vesicle).

Isoperla sordida, Banks, 1907a:13.

Isoperla sordida, Claassen, 1940, 232:206.

Isoperla sordida, Illies, 1966:420.

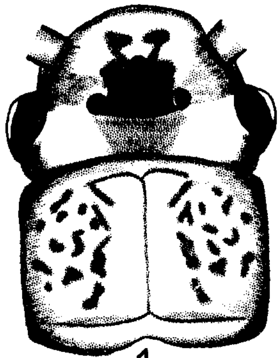
Isoperla sordida, Zwick, 1973:251.

Additional references: _Isoperla sordida_, Needham and Claassen, 1925 (male and female genitalia); Hoppe, 1938; Jewett, 1956, 1959, and 1960 (male and female genitalia); Gaufin, 1964b (in part); Knight et al., 1965b (ova); Gaufin et al., 1966 (in part, male and female genitalia); Newell, 1970; Gaufin et al., 1972 (in part, male and female genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (in part, male and female genitalia).

Description (Plates XXIV and XXVII)

Male (Pl. XXVII).-- Macropterous. Length of forewings 9.0-10.4 mm; length of body 9.0-10.0 mm. General body color dark brown. Interocellar space of head dark brown, forming equilateral triangle between ocelli, 2 hook-shaped, narrow, dark brown bands extending toward clypeus; medium brown triangular band connecting lateral ocelli to occiput; light brown band extending from interocellar triangle to base of antennae and front of eyes (Fig. 1). Pronotum light

Plate XXVII, Figs. 1-7. _I. sordida_. 1. adult head and pronotum (scale: 1 mm = .09 mm). 2. male vesicle and 8th sternum (1 mm = .05 mm). 3. sclerotized aedeagal process, dorsal aspect (1 mm = .01 mm). 4. male paraproct, lateral aspect (1 mm = .03 mm). 5. female subgenital plate (1 mm = .05 mm). 6. male aedeagus, lateral aspect, A. anteroventral lobe, B. small mesoposterior lobe, C. patch of concentrated, small, stout spinulae, D. large dorsal lobe, E. sclerotized process (1 mm = .02 mm). 7. sclerotized aedeagal process, lateral aspect (1 mm = .001 mm).



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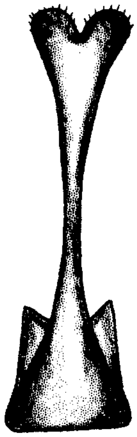

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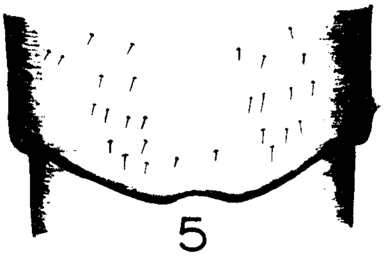

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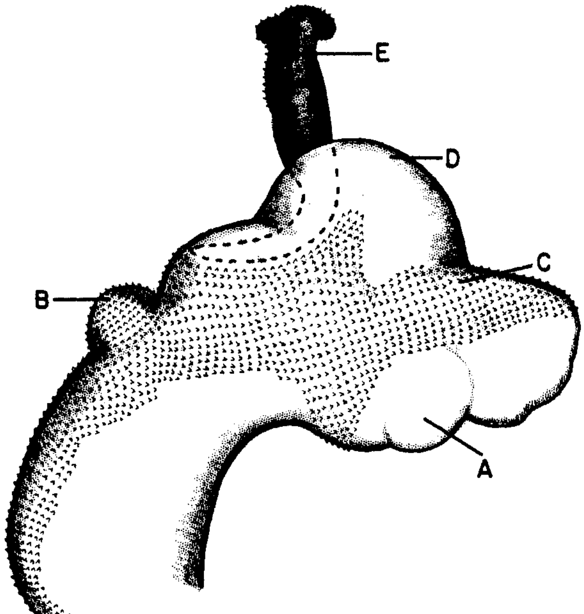

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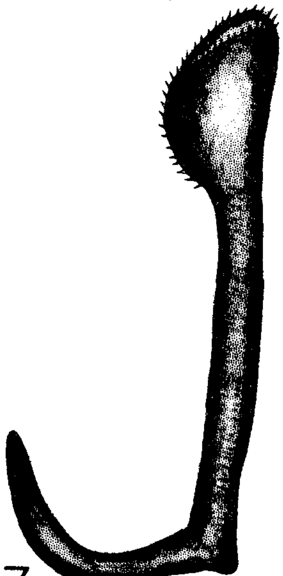

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brown, median yellow stripe, numerous vermiform, dark brown rugosities (Fig. 1). Wings flavescent, veins dark brown. Abdominal terga with 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Paraprocts thin, elongate, tapering to long, fine points apically; small, fine hairs scattered on upper surface, recurving over 1/4 10th tergum (Fig. 4). Cerci with one long, fine ventral hair at posterior margin of each segment. Vesicle elongate, narrow at base, rounded at apex, lighter than rest of segment (Fig. 2). Aedeagus with large dorsal lobe void of spinulae (Fig. 6D), with stout sclerotized process; dorsal arm bifurcate at tip, apex of each arm rounded and bearing row of small, stout spines (Figs. 3, 6E, & 7); anterodorsal margin produced into large lobe with dorsal patch of small, stout spinulae (Fig. 6C), smaller ventral lobe void of spinulae (Fig. 6A), small median posterior lobe covered with small, stout spinulae (Fig. 6B); large patch of small, stout spinulae covering posterior and lateral aedeagus surfaces, extending along top half anterior lobe (Fig. 6C).

Female (Pl. XXVII).-- Macropterous. Length of forewings 10.5-13.1 mm; length of body 10.4-13.0 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate indistinct, broad at base, evenly rounded posteriorly, with median shallow emargination, produced 1/4 length of 9th sternum (Fig. 5).

Nymph (described from female nymphal exuviae) (Pl. XXVII).--

Length of mature female nymph 15-16 mm. Ocelli of head connected by band of dark brown pigmentation, band forming dark, equilateral triangle between ocelli, small light interocellar spot; wide, dark brown band extending from top of compound eyes and base of antennae to ocellar triangle; large "U"-shaped light area in front of anterior ocellus; occipital ridge bearing small, stout spinulae. Pronotum medium brown, median yellow stripe, 1 wide medium brown band, with variable light areas, bordering median stripe, margin fringe with short, stout setae, occasional long hairs interspersed at lower angles. Femora, tibiae, and tarsi with dorsal fringe of long, fine hairs, outer surface of femora with scattered spine-like setae, tibiae with ventral row of spine-like setae. Abdominal terga with 3 longitudinal stripes, 2 lateral and one mesal, and 8 faint rows of longitudinal dots, 2 mesal, and 3 each laterally. Posterior margin of cercal segments with whorl of small, stout hairs and one long ventral hair.

Ova (Pl. XXIV).-- General shape oval, cross section circular (Fig. 9). Color light brown. Length .32 mm; width .23 mm. Collar developed, expanded slightly at apex with elevated ridges (Figs. 9 & 11). Chorionic ridges elevated, forming hexagonal cells, each with numerous, evenly spaced, small punctations (Figs. 9-11). Micropyles arranged 2 or 4 on top of distinct, elevated, transverse pollar ridge, extending through hexagonal cells near bottom

1/3, on one side; raised, elongate sperm guides below each micropyle (Fig. 10).

Material examined.-- TYPES: *I. sordida*, Holotype ♀, USA, CALIFORNIA: Los Angeles Co., Date ?, Hutchinson (MCZ #11,338). Additional specimens - USA - CALIFORNIA: Los Angeles Co., L. Elizabeth Can., 26/IV/1950, Collector ?, 1♂, 1♀ (LCMNH); Trinity Co., E. C. Van Dyke, 2♂, 2♀ (CAS). MONTANA: Carbon Co., Rock Crk., Hell Roaring Crk., 29/VII/1966, J. R. Grierson, 1♂ (RWB); Glacier Co., Glacier Park, Siyeh Crk., 9/VIII/1963, Collector ?, 2♂ (RWB), Glacier Park., Siyeh Crk., 13/VIII/1963, Collector ?, 1♂, 1♀ (RWB), Waterton R., 23/VII/1970, C. Yarmoloy, 1♂ (RWB); Ravalli Co., 4.3 mi. above Hwy. 93, Chaffin Crk., 6/VII/1965, J. R. Grierson, 2♀ (UU), 1 mi. above Cameron Crk., Hart Crk., 23/VI/1965, J. R. Grierson, 1♂ (UU). OREGON: Deschutes Co., Fall R., 7/VI/1949, S. G. Jewett and Morton, 1♂, 1♀ (LCMNH), Fall R., 13/VII/1948, S. G. Jewett, 15♀, 10 nymphs (SGJ); Jefferson Co., Wizard Falls, Metolius R., 19/IX/1949, L. E. Perry, 1♂, 1♀ (RWB), Wizard Falls, Metolius R., bridge near clear lake, 7/IX/1965, S. G. Jewett, 1♀ (USNM); Sherman Co., Sheep Bridge, Deschutes R., 16/IX/1948, S. G. Jewett, 6♀, 2 exuviae (CAS); Wallowa Co., Wallowa Mts., Lost Lake, 18/VIII/1952, K. M. Fender, 2♂, 2♀ (CAS), Crawfish Lake, trail above Anthony Lake, 12/VIII/1972, K. M. Fender, 1♂, 2♀ (CAS), Lake Crk. Camp, Lastine R., 19/VIII/1952, K. M. Fender, 3♂ (CAS).

Distribution.-- CANADA: British Columbia; USA: California, Montana, Oregon, and Washington (Fig. VIII).

Diagnosis and Discussion

_I_. _sordida_ is closely related to _I_. _denningi_. Males can be distinguished by the completely dark interocellar area of the head, shorter, stouter, vesicle longer, thinner, more acute paraprocts, longer, narrower sclerotized process of the aedeagus bearing short spines on apex of short, rounded arms, and lack of large dorsal expand aedeagus lobe covered with small, stout spinulae. Females can be differentiated by the completely dark interocellar area of the head, and much shallower, evenly rounded subgenital plate. The nymph of _I_. _denningi_ is unknown. Ova can be distinguished by the large size, elevated chorionic ridges, elevated micropyle ridge, and raised sperm guides,

There has been some confusion regarding the original generic placement of this species, and it has been incorrectly cited since its inception. Banks (1906a) originally placed the species in the genus _Isoperla_, although at that time he had grouped the _Isoperla_ in the family Perlidae. In his catalogue (Banks 1907), it was cited as _Isoperla sordida_ Banks (_Perla_), which was apparently an error. The sex of the type specimen has also been confused in the literature. The holotype in the Harvard collection is a male specimen, and the illustration (Fig. 5, ventral plate) in the original paper is the male vesicle of the 8th sternum, not the female subgenital plate.

This is a rare species, and no biological studies have been made. Based on the material examined, emergence occurs late-Apr. until early Sep., in creeks and small rivers.

Cascadoperla NEW GENUS

Perla Hoppe, 1938, 4:151.

Isoperla Frison, 1942, 22:336.

Isoperla Illies, 1966:422.

Isoperla Zwick, 1973:252.

Type species - *Isoperla trictura* (Hoppe), 1938, 4:151, herein designated.

Description (Plates VI and XXVIII)

Adult (Pl. XXVII).-- Body length: medium (8.0-11.5 mm). Wings: macropterous, hyaline, veins medium brown, venation typical for the genus *Isoperla*. Gills: absent from thorax or abdomen. Pronotum: median light stripe, bordered by 2 longitudinal dark brown bands. Mesosternum: arms of "Y"-shaped mesosternal ridge attached to posterior end of furcal pits, transverse ridge connecting anterior tips of furcal pits. Body color: yellow to light brown. Abdominal terga: 3 longitudinal dark stripes, 1 mesal and 2 lateral.

Male terminalia.--Ninth tergum: bipartite median patch of short, stout spinulae and dark pigmentation, mesoposterior margin elevated, with inverted "V"-shaped medium brown band. Tenth tergum: partial cleft extending from posterior margin, posterolateral margins of cleft developed into elongate, tapered, sclerotized genital hooks. Vesicle: absent. Paraprocts: joined at base, not connected to base of cerci, weakly sclerotized, blade-like, rounded at tips and produced 1/4 length over 10th tergum. Aedeagus: entirely membranous, tubular, bearing patches of small and long, hair-like spinulae.

Female terminalia.-- Subgenital plate: reduced to a small median nipple on posterior margin of 8th sternum. Vagina: lined with small, stout spinulae, 7 long, tubular accessory receptacular glands attached to seminal receptacle; seminal receptacle a rounded, membranous sac.

Nymph.-- Body length: medium (9.1-12.6 mm). Body color: light yellow. Pronotum: median light stripe, bordered by 2 wide, medium brown longitudinal bands, fringed with small stout hairs, numerous long hairs irregularly placed at upper and lower angles and posterior margin. Gills: absent from submentum, thorax, and abdomen. Laciniae: apical and subapical teeth, subapical tooth ca. 3/4 length of apical tooth, bush of long, stout hairs on elevated, evenly rounded ridge below subapical tooth, 3 long, stout spines on inside margin below subapical tooth. Labrum: wide, evenly rounded median hump, lateral and anterior margins fringed with long, fine hairs. Mandibles: typical, as described for *Isoperla*. Labium: typical, as described for *Isoperla*. Mesosternum: typical, as described for *Isoperla*. Proventriculus: typical, as described for *Isoperla*. Abdominal terga: typical, as described for *Isoperla*.

Ova.-- General shape: oval. Cross section: 9-sided polygon. Collar: well developed, expanded apically, forming large, flat top. Chorion: striate, 9 elevated longitudinal ridges, connected by lower transverse ridges, appearing ladder-like, forming large quadrangular-shaped pockets. Micropyles: arranged singularly on top of longitudinal ridges, near bottom 1/3 (Fig. 3).

Diagnosis and Discussion

Cascadoperla is a montypic genus. It shares the following characters with the *Isoperla*: 1. absence of gills or gill remnants on adult and nymphal thoracic and abdominal sterna; 2. fork of 2nd anal vein of forewings included in anal cell, so that its branches leave the cell separately; 3. arms of the "Y"-shaped mesosternal ridge in nymphs and adults attached to posterior end of furcal pits, and transverse ridge connecting anterior tips of furcal pits; 4. nymphal proventriculus with 26-27 longitudinal rows of sharp, posterior projecting spines; 5. 6-7 accessory receptacular glands attached to seminal receptacle or receptacular duct, vaginal floor with variable spinule patch; and 6. abdominal terga with 3 longitudinal stripes, 1 mesal and 2 lateral.

It differs from the Isoperla by the following characters: 1. posteromesal hump and bipartite patch of spinulae of the 9th tergum in adult males; 2. partial cleft and genital hooks of the 10th tergum; 3. lightly sclerotized, blade-like paraprocts, rounded at tips, contigous at base and not connected to the base of cerci; 4. absence of vesicle from posteromedian margin of male 8th sternum (also absent in I. ebria); 5. reduced, nipple-like female subgenital plate on posteriomedian margin of 8th sternum; 6. presence of numerous, long, fine hairs on margin of the pronotum; 7. wide median hump on nymphal labrum; 8. bush of long, stout hairs and 3 long, stout spines on elevated ridge of nymphal laciniae; 9. continuous row of long dorsal and ventral hairs after 10th cercal segment; and 10. ova striate, with 9 longitudinal elevated ridges, connected by lower transverse ridges, forming large quadrangular pockets, each bearing numerous, minute punctations.

This genus is closely allied with Calliperla Banks, sharing lightly sclerotized paraprocts, genital hooks developed from posterior margin of 10th tergum, and spinule patch on posterior 1/2 of 9th tergum. It differs by the lack of supraanal process, absence of vesicle on 8th sternum, cleft of 10th tergum, and greatly reduced subgenital plate. Both genera have retained characters of an

Isogenus ancestor, such as the cleft and development of genital hooks from the posterior margin of the 10th tergum. These genera, plus the genus *Rickera* Jewett, probably represent transitory stages in the development and evolution of the *Isoperla* from *Isogenus*.

Cascadoperla is distributed throughout the Coastal and Cascade Mountain Ranges of the Pacific Coast, and also has limited distribution in the Northern Rocky Mountains of Idaho and Montana (Fig. IX). *Cascadoperla trictura* inhabits creeks and rivers, and emergence continues from mid-May until late Jul.

Etymology.-- This genus name is taken from the Cascade Mountain Range of the Pacific Coast, where it is quite abundant.

Cascadoperla trictura (Hoppe)

Perla trictura Hoppe, 1938, 4:151. Holotype ♂, and allotype ♀, Maple Valley, Cedar R., King Co., Washington, USA (TBM) (male and female genitalia).

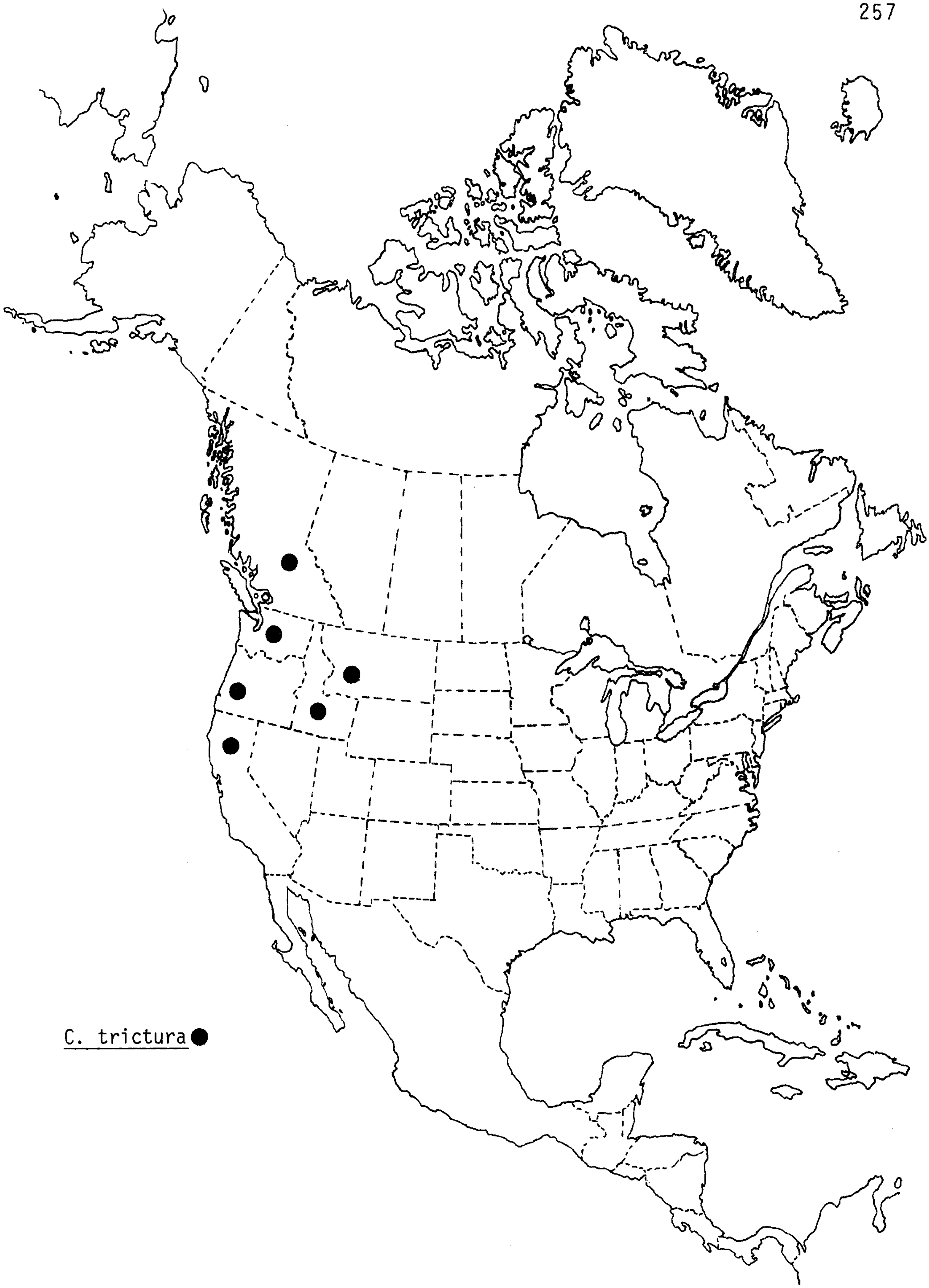
Isoperla trictura, Frison, 1942, 22:336 (adult male head-pronotal pattern, and male and female genitalia).

Isoperla trictura, Illies, 1966:422.

Isoperla trictura, Zwick, 1973:252.

Additional references: *Isoperla trictura*, Ricker, 1943; Jewett, 1959 and 1960 (male and female genitalia); Gaufin, 1964; Knight et al., 1965b (ova); Gaufin et al.,

Fig. IX. Distribution of the genus Cascadoperla

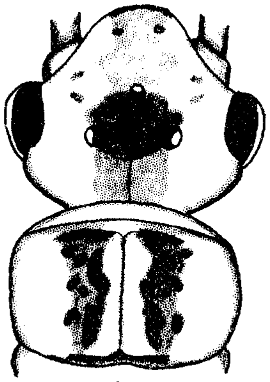

C. trictura

1972 (male genitalia); Ricker and Scudder, 1975; Baumann et al., 1977 (male and female genitalia).

Description (Plates VI and XXVIII)

Male (Pl. XXVIII).-- Macropterous. Length of forewings 8.0-9.5 mm; length of body 8.0-9.0 mm. General body color yellow to light brown. Round black spot covering inter-ocellar area of head; wide medium brown band extending from occiput, through spot, and continuing to anterior margin of frons (Fig. I). Pronotum light yellow, median light stripe bordered by 2 longitudinal dark brown bands containing vermiform rugosities (Fig. I). Meso- and metanota dark brown, median light yellow stripe of pronotum extending 1/2 length of mesonotum. Wings hyaline, veins medium brown. Abdominal terga with 3 longitudinal dark brown stripes, one mesal and 2 lateral; 8 rows of longitudinal dots, 2 mesal and 3 each laterally. Ninth tergum with bipartite median patch of short, stout spinulae and dark pigmentation, mesoposterior margin elevated, with inverted "V"-shaped medium brown band (Figs. 3 & 7). Tenth tergum with partial cleft, extending from posterior margin; posterolateral margins of cleft developed into elongate, tapered, sclero-tized, genital hooks, appearing stout laterally, extending to anterior margin of segment (Figs. 3 & 7B). Posterior margin of cercal segments with a long ventral hair. Vesicle absent. Paraprocts joined at base, not connected to base of

Plate XXVIII, Figs. 1-8. *Cascadoperla trictura*. 1. adult head and pronotum (scale: 1 mm = .08 mm). 2. nymph head and pronotum (1 mm = .08 mm). 3. male terminalia, dorsal aspect (1 mm = .02 mm). 4. male aedeagus, lateral aspect, A. posteroventral band of small, fine spinulae, B. posterodorsal patch of long, fine, hair-like spinulae, D. dorsal nipple-like lobe (1 mm = .02 mm). 5. nymphal labrum (1 mm = .02 mm). 6. nymphal left maxilla, A. stipe, B. lacinia, C. apical tooth (1 mm = .03 mm). 7. male terminalia, lateral aspect, A. paraprocts, B. genital hooks, C. median bipartite spinulae patch of 9th tergum (1 mm = .02 mm). 8. female 8th sternum with mesoposterior nipple-like subgenital plate (1 mm = .04 mm).



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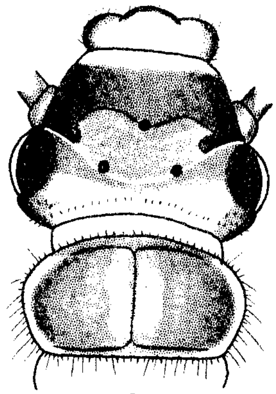

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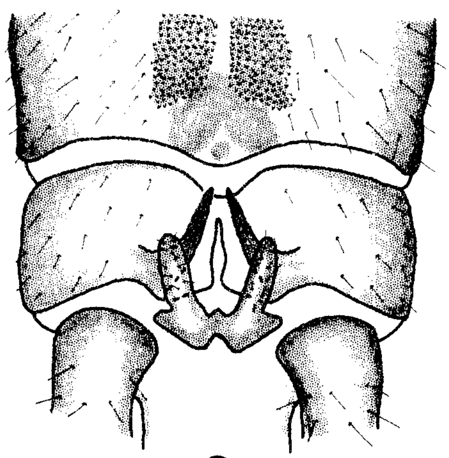

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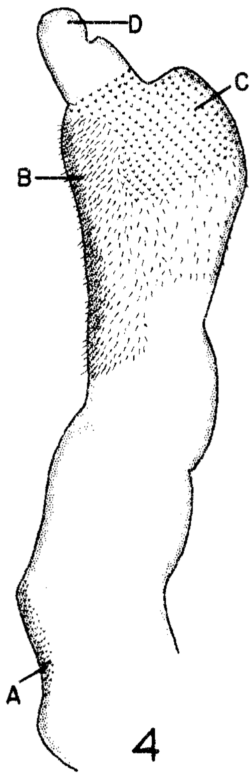

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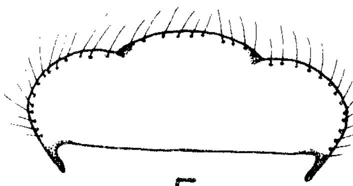

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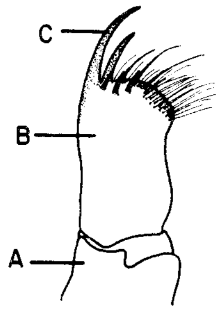

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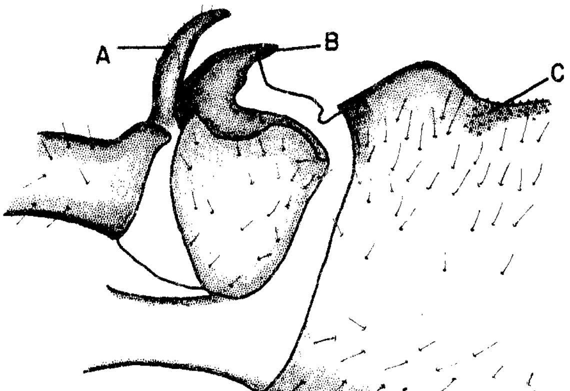

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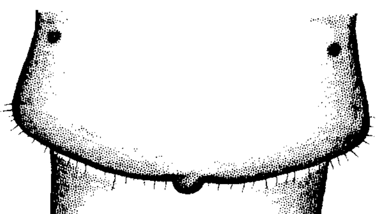

8

cerci, slightly sclerotized, rounded at tips, slightly tapered, dorsal surface bearing fine hairs, produced 1/4 length of 10th tergum just beyond base of genital hooks (Figs. 3 & 7A). Aedeagus completely membranous, tubular, nipple-like lobe at apex void of spinulae (Fig. 4D), anterodorsal section expanded slightly, bearing patch of concentrated, small spinulae extending to posterior base of nipple-like lobe (Fig. 4C), posterodorsal margin bearing concentrated patch of long, fine, hair-like spinulae, extending to mid-length and to anterior margin, below patch of small spinulae (Fig. 4B), proximal stalk void of spinulae except narrow band of very small, fine spinulae at posteroventral margin (Fig. 4A).

<u>Female</u> (Pl. XXVIII).-- Macropterous. Length of forewings 9.5-11.0 mm; length of body 10.0-11.5 mm. General body color and head-pronotal pigment patterns similar to male. Subgenital plate reduced to small mesoposterior nipple on 8th sternum; darker than rest of segment; posterior margin of 8th sternum broadly rounded, with fringe of fine, medium-length hairs (Fig. 8).

<u>Nymph</u> (Reared) (Pl. XXVIII).-- Length of mature male nymph 9.1-10.3 mm; length of mature female nymph 10.2-12.6 mm. Interocellar area of head medium brown, wide, dark brown pigment band extending across frons; anterior margin with narrow, light transverse band, row of small, stout spinulae on occipital ridge (Fig. 2). Pronotal margin

fringed with small, stout hairs, numerous long hairs irregularly placed at upper and lower angles and posterior margin; angles broadly rounded; median light yellow stripe bordered by 2 wide, medium brown longitudinal bands; rugosities absent; light narrow band on lateral and posterior margins (Fig. 2). Labrum with wide, evenly rounded median hump, lateral and anterior margins with fringe of long, fine hairs (Fig. 5). Laciniae with apical and subapical teeth; subapical tooth approximately 3/4 length of apical tooth; bush of long, stout hairs on elevated, evenly rounded ridge below subapical tooth; 3 stout spines on inside margin below subapical tooth (Fig. 6). Mandibles and labium typical, as described for western Isoperla. Proventriculus with 26-27 longitudinal rows of sharp posterior projecting spines. Femora, tibiae, and tarsi with dorsal fringe of long, fine hairs; ventral fringe of long, fine hairs on tibiae; scattered stout spines on outer surface of femora and tibiae. Abdominal terga with 3 longitudinal dark stripes, 1 narrow mesal and 2 wide lateral stripes. Posterior margin of cercal segments with whorl of small, stout setae, continuous row of long dorsal and ventral hairs after 10th segment.

Ova (Pl. VI).-- General shape oval, cross section 9-sided polygon (Figs. 1 & 2). Color light brown. Length .30 mm; width .18 mm. Collar well developed, expanded apically, forming large flat top (Figs. 1, 2, & 7). Chorion striate, with 9 elevated, longitudinal ridges connected by lower transverse ridges, appearing ladder-like, forming large quadrangular-shaped pockets (Figs. 1-3). Micropyles arranged singularly on top of longitudinal ridges near bottom 1/3 (Fig. 3).

Material examined.-- Paratypes, WASHINGTON: King Co., Maple Valley, Cedar R., 27/V/1973, G. N. Hoppe, 2♂ (INHS), Kittitas Co., Cle Elum, 15/VII/1932, G. N. Hoppe, 1♀ (INHS). Additional species - CANADA - BRITISH COLUMBIA: Vedder Crossing, 11-19/V/1937, W. Ricker, 2♂ (INHS), Cultus Lake, 12/V/1939, W. Ricker, 1♂, 1♀ (INHS), Cultus Lake, Lower Sweltzer Crk., 12/V/1937, W. Ricker, 8♂, 2♀ (WR), Cultus Lake, Chilliwack R., 8-22/V/1938, S. Spender, 2♂ (INHS), Cultus Lake, Lower Sweltzer Crk., 12/IV/1941, W. Ricker, 8♂, 4♀ (INHS), Cultus Lake, Sweltzer Crk., 19/II/1939, W. Ricker, 22 , 6 nymphs (INHS). USA - CALIFORNIA: Madera Co., Oakhurst, 26/V/1942, A. J. Watz, 1♂ (CAS); Yosemite Co., Yosemite Valley, 5/VII/1927, E. J. Nast. 1♂ (CAS). MONTANA: Ravalli Co., Hwy. 93, 1.5 mi. N. of Hamilton, Bitterroot R., 23/VII/1965, 2♀ (RWB). OREGON: Benton Co., 9 mi. N. of Corvallis, Berry Crk., 16/V/1960, Collector ?, 1♂, 1 exuvia (SGJ), Alsea R., 24/V/1939, Pillow, 1♀ (INHS), Hwy. 34 above Alsea, Rock Crk., 27/V/1977, S. W. Szczytko and K. W. Stewart, 4♂, 2♀, 1 nymph (SWS & NTSU), Oak Crk., 4/V/1934, E. E. Ball, 2 nymphs (INHS), Kings Valley Trib. of Luckiamute R., 11/V/1933, Prentiss and Dimick, 1 nymph

(INHS); Clotsap Co., Necanicum R., 14/VI/1948, S. G. Jewett, 2♂ (BS), Youngs R., 10/V/1947, S. G. Jewett, 1♂ (OS^{2}), Necanicum R., 13/VI/1948, S. G. Jewett, 3♂ (SGJ), Big Crk., 28/V/1949, S. G. Jewett, 35♂, 33♀ (SGJ); Clackamas Co., Mollala R., 13/VI/1948, S. G. Jewett, 1♂ (INHS); Linn Co., Lacomb, Crabtree Crk., 4/VI/1935, R. Dimick, 1♂ (INHS); County ?, Willamette R., 26/V/1938, C. Jensen, 1♀ (INHS). WASHINGTON: Grays Harbor Co., Hamptulips, Hwy. 101, Hamptulips R., 18/VI/1967, R. W. Baumann, 1♂ (RWB); King Co., Cedar Falls, Cedar R., 22/VI/1972, J. Malick, 2♂, 2♀ (BS).

Distribution.-- CANADA: British Columbia; USA: California, Idaho, Montana, Oregon, and Washington (Fig. IX).

Diagnosis and Discussion

This species is distinctly unlike any described species of *Isoperla*. Males can be separated from all *Isoperla* by the head-pronotal pigment pattern, general yellowish body color, posteromesal hump of the 9th tergum, partial cleft of the 10th tergum and development of tapered sclerotized genital hooks from posterolateral margins of the cleft, lightly sclerotized paraprocts joined at the base, rounded at the tips and not connected to the base of the cerci, absence of a vesicle from the 8th sternum (also absent in *I. ebria*), and long, tubular aedeagus with apical nipple-like lobe. Females can be distinguished by the distinctive head-pronotal pigment pattern, general yellowish body color, and the reduced nipple-like subgenital plate. Nymphs can be separated by the distinctive head-pronotal pigment pattern, numerous long, fine hairs on the pronotum, wide, evenly rounded median hump of the labrum, bush of long, stout hairs on an elevated, evenly rounded ridge below subapical tooth of the laciniae, presence of 3 long, stout spines on inside margin below subapical tooth, and presence of a continuous row of long dorsal and ventral hairs after the 10th cercal segment. Ova can be distinguished by the deeply incised, striate chorion with 9 longitudinal ridges connected by lower, transverse ridges appearing ladder-like and forming large, quadrangular pockets, expanded apical section of the collar forming large, flat top, and by the numerous minute chorionic punctations.

The life history and general biology of this species are unknown. Based on the material examined, emergence occurs from mid-May until Jul. in creeks and rivers.

CHAPTER IV

DISCUSSION

This revision of the western Nearctic *Isoperla* provides a foundation for further analysis of the entire holarctic subfamily. Holomorphology of the 21 western species has revealed 6 distinct morphological species complexes, unique in characters of the male aedeagus and ova.

The *I. quinquepunctata* complex (A) is thought to be the least specialized group, exhibiting an entirely membranous aedeagus, usually bearing tubular dorsal processes, patches of long, stout hairs or spinulae on the 9th and/or 10th male abdominal terga, and ova uniformly punctate without elevated chorionic ridges. *I. katmaiensis* is closely related, but was left unassigned to a group because of its unique unsculptured and ornate collared ova.

The *I. phalerata* complex (B) shows little additional specialization of the aedeagus, but the ova in both species have developed elevated chorionic ridges and enlarged micropyles, highly ornate and elevated in *I. pinta*, with multiple openings. The membranous aedeagus and spinule patches on the male 9th tergum ally this group with the *I. quinquepunctata* complex and *I. katmaiensis*.

The *I. ebria* complex (C) exhibits intermediate specialization in aedeagal armature, and 2 of the species, *I. ebria* and *I. tilasqua*, bear patches of long, stout hair-like spinulae on the posterior margin of the aedeagus. The ova seem also to exhibit intermediate specialization, with elevated ridges forming hexagonal-shaped cells (absent in *I. ebria*), and well-developed collars. This complex is not closely related to any other, except *I. phalerata*.

The *I. marmorata* complex is further specialized, all species having an aedeagal sclerotized process and thickened chorionic ridges, forming irregular shaped depressions in the ova. The *I. sordida* complex represents the most advanced group and has the largest number of species. Further specialization is suggested by the highly modified, forked sclerotized aedeagal process, and variable ova characters. Several species (*I. adunca* and *I. bifurcata*) have collarless, ornate ova, and others (*I. petersoni* and *I. sordida*) have elevated, transverse micropyle ridges.

The Isoperlinae are closely related to, and probably developed from, the Perlodinae. Several primitive genera in the Isoperlinae, *Cascadoperla*, *Calliperla*, and *Rickera*, have retained important morphological features common in the Perlodinae, and represent transitory stages in the development and evolution of the *Isoperla*. In *Cascadoperla* the male terminalia are remarkably similar to most Perlodinae in that the 10th tergum is cleft and bears a pair of long genital hooks (10th tergum is uncleft in *Diura*). *Calliperla* has retained the epiproct of the Perlodinae (epiproct is absent in *Diura*) although it is short and unsclerotized, and in *Rickera* the male vesicle is located on the 7th abdominal sternum, which is common in all Perlodinae.

Isoperla therefore appears to be the most advanced genus in Isoperlinae, having lost typically Perlodinae characters, such as the cleft and genital hooks of the male 10th tergum, male epiproct, and movement of the male vesicle from the 7th to 8th abdominal sternum. A *Diura*-type ancestor is probable for *Isoperla*, but must remain a pertinent question until further holomorphological study of all genera of Perlodinae and Isoperlinae, as I have done for this 21-species western Nearctic *Isoperla* segment.

The Isoperlinae differ from the Perlodinae by the following characters: 1. 10th tergum entire (partially cleft in *Cascadoperla*); 2. genital hooks from 10th tergum absent (present in *Cascadoperla*), 3. paraprocts sclerotized and variously developed; 4. epiproct absent (present but weakly developed in *Calliperla*); 5. male vesicle present on 8th abdominal sternum (present on 7th sternum in *Rickera*); 6. ova usually round and sculptured (unsculptured in *I. katmaiensis*); 7. submental, thoracic, and abdominal gills absent; and 8. three longitudinal stripes on abdominal terga. These character differences are major, and if substantiated by further holomorphological study of the subfamily, they will undoubtedly prove of sufficient magnitude to justify return of the group to family status, as proposed by Frison (1942).

The male aedeagus, and ova, were found to contain the diagnostic characters for group and species separation. It is therefore suggested that collectors attempt to extrude aedeagii in male specimens at time of collections to facilitate identification. Ova were most useful in species separation but had limited use in separation of groups. Of course, SEM preparation is not always convenient or feasible for some field studies. Essentially, no substantive intra-species geographic variation was noted in the aedeagal characters of general shape, spinule patterns, shapes and sizes of spinulae, and presence or shapes of the sclerotized process, or the ova characters of size, shape, chorionic ridges and punctations, collar, and micropyle grouping and accessory structures (such as transverse ridges, elevated ornate structures, and sperm guides). Separation of females is difficult because of interspecific similarities of the subgenital plate and its great intraspecific variation. The presence, absence, or degree of the mesoposterior emargination was always a variable character in any population. Head and pronotal pigment patterns are the most reliable external characters, but their phylogenetic significance is obscure. The vagina was not diagnostic at the species or generic levels. All species exhibited 6-7 tubular accessory receptacular glands attached to the seminal receptacle or receptacular duct, vaginal cavity lined with variable spinulae, and the seminal receptacle membranous and variably shaped.

The wings offered little value for generic, group, or species separation. Vein variation was noted within and between populations. In several species, wing color was used to distinguish closely related species. It appears from this study that wing length is not a characteristic of the species, but rather of the environment.

Combinations of color patterns and setation of the cerci, legs, pronotum, and occipital ridge were used for differentiation of nymphs. The nymphal proventriculus was not diagnostic for species separation or for separation of Isoperla and Cascadoperla. All species possessed 23-26 variable longitudinal rows of stout posterior projecting spinulae. I was disappointed in the lack of inter-specific variation, and therefore diagnostic value, of the nymphal mouthparts of these western species, especially in light of great variation noted in eastern species I have studied (Szczytko and Stewart 1976, 1977, and 1978). Generic differences in the laciniae and labrum were diagnostic between the western Isoperla and Cascadoperla. The mesosternal ridge was consistent throughout all species, in that the arms of the "Y"-shaped ridge attached to the posterior end of the furcal pits and a transverse ridge connected the anterior tips of the pits.

Color patterns of the nymph and adults were useful in differentiating species, when used in combination with other characters. Some geographic variation was noted for each species, and striking color patterns of fresh material soon fade after a few years in preservative.

Data on the biology and life histories of these western Isoperla species is meager or nonexistent. This is surprising, since most species appear to be important, integral, functioning components of the benthic communities of western lotic systems (Fuller and Stewart 1977 and 1978; Stanford, unpublished Ph.D. dissertation). Data generated from such studies would also be useful in phylogenetic interpretations according to Henning's (1966) concept of holomorphology, and the importance placed on life history events patterns by Ross (1974).

This study involved 2 extensive field collecting trips, and examination of over 5,000 specimens from all available university, museum, and individual collections. However, several areas have received little collecting effort. Generally, specimens from Alaska, California, Northwest Territories, Washington, and the Yukon are poorly represented. These areas are very interesting from a zoogeographic and past dispersal standpoint, since they contain a number of endemic species, and may have been Pleistocene refugia (Ricker 1964). Of the 8 remaining undescribed nymphs, 6 are endemic to this region, and the other 2 are common. Future collection and rearing of these nymphs should receive high-priority attention, enabling completion of the nymphal key and providing additional phylogenetic data.

I. katmaiensis is known only from the Alaskan Katmai Peninsula, and is probably an Alaskan refugium species. The primitive genera (*Cascadoperla*, *Calliperla*, and *Rickera*), and the more advanced *I. sordida* complex, are restricted mainly to the Pacific Coast, Cascade Ranges, with limited distribution in the Northern Rocky Mountains, suggesting they were derived from ancestors surviving the ice cover during the Pleistocene, below 48^{o} N in those areas, or in the Alaskan refugium (Ricker 1964). Subsequent dispersal eastward into the northern Rockies have probably been along major river systems such as the Snake. *I. jewetti* is apparently a relict population or recently evolved species in stressed southern range limits (Texas and Colorado), and *I. longiseta* has successfully dispersed eastward into stressed grassland biome streams (Ricker 1964). The wide range of *I. longiseta* suggests a high vagility and wide tolerance to stress conditions. The remaining species are distributed from the Rocky Mountains to the Pacific Coastal Ranges in a wide variety of lotic habitats.

CHAPTER V

SUMMARY

1. This holomorphological study of all life stages of western Nearctic stoneflies in the genus *Isoperla* was conducted over the 3-year period 1975-1978. Over 5,000 specimens from all available University, museum, and individual collections were studied.
2. An NSF Doctoral Dissertation Improvement Grant enabled two extensive field collecting-rearing trips during the seasonal emergence times of *Isoperla* in May, 1976 and May-Jun., 1977. Streams in New Mexico, Colorado, Wyoming, and Utah were collected in 1976. Different localities in these states were visited in 1977, and streams in the Coastal and Cascade Mountain ranges were collected in Oregon and Washington in 1977.
3. One monotypic genus new to science, *Cascadoperla*, is described, and *Cascadoperla trictura* (Hoppe) designated as the type species. The nymph, adult male and female, and ova are described and illustrated. Live nymphs were collected in Oregon in 1977, and successfully reared for the first time.
4. Three species new to science, *I. bifurcata*, *I. katmaiensis*, and *I. tilasqua* were discovered. Detailed descriptions are given for both adult sexes and the ova. *I. bifurcata* males and females were collected in Oregon in May, 1977.

5. The 21 species are arranged into 5 distinct complexes, and one unassigned species, primarily on the basis of male aedeagus and ova characters:

A. The *I. quinquepunctata* complex is composed of *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, and *I. quinquepunctata* (Banks). All species share an entirely membranous aedeagus, usually bearing tubular dorsal processes, patches of long, stout hairs or spinulae on the 9th and/or 10th male abdominal terga, and ova uniformly punctate, without elevated chorionic ridges.

Unassigned -- *I. katmaiensis* is closely related to the *I. quinquepunctata* complex. It is characterized by an entirely membranous aedeagus with 2 long, tubular dorsal processes, male 9th tergum with posterior bipartite patches of stout spinulae, and ova with non-sculptured chorion and ornate collar.

B. The *I. phalerata* complex is composed of *I. phalerata* (Needham) and *I. pinta* Frison. Its members are characterized by an entirely membranous, highly lobate aedeagus, male 9th tergum with either a single or bipartite patch of stout spinulae, male vesicle reduced, sharply tapered paraprocts with acute ventral spine, and ova with well-developed chorionic ridges and enlarged micropyles.

D. The *I. ebria* complex is composed of *I. sobria* (Hagen), *I. gravitans* (Needham and Claassen) and a new species *I. tilasqua*. Its members have an entirely membranous tubular aedeagus bearing one or more patches of long, hair-like spinulae, ova with developed chorionic ridges forming hexagonal-shaped cells, and large body size and dark pigment patterns.

D. The *I. marmorata* complex is composed of *I. fulva* Claassen and *I. marmorata* (Needham and Claassen). It is characterized by an aedeagus bearing a club-shaped sclerotized process, with small spines at the apex, broadly rounded, shallow male vesicle, and ova with elevated, thickened chorionic ridges forming irregular-shaped depressions.

E. The *I. sordida* complex is composed of *I. acula* Jewett, *I. adunca* Jewett, *I. denningi* Jewett, *I. fusca* Needham and Claassen, *I. petersoni* Needham and Christenson, *I. rainiera* Jewett, *I. sordida* Banks, and a new species *I. bifurcata*. They are characterized by a variably produced aedeagal process, forked at the base with a modified dorsal arm usually forked (not forked in *I. adunca*, *I. rainiera*, or *I. petersoni*), and ova usually with well-developed chorionic ridges (ridges absent in *I. denningi*) and variable collar (collar absent in *I. adunca* and *I. bifurcata*).

5. Six nymphal descriptions new to science are provided, with illustrations (nymph of *I. sordida* described from

exuviae; no illustrations) including *I. longiseta*, *I. marmorata*, *I. mormona*, *I. phalerata*, *I. rainiera*, and *Cascadoperla trictura*. An example of rearing success was collection of *I. rainiera* nymphs from a snow-fringed stream at mm elevation on Mt. Hood, Oregon, successful transport to Texas, and rearing of 5 individuals in an environmental chamber.

6. Complete descriptions of ova, with accompanying SEM photographs, are provided for 20 species of *Isoperla* (females and ova are unknown for *I. acula*), and the one species of *Cascadoperla*. Eleven of these are described for the first time.

7. Two species are placed in synonymy. I. patricia was found to be a synonym of *I. quinquepunctata* (Banks), based on similarities of adult and nymphal pigment patterns and other shared characters, especially the ova and aedeagii. Detailed comparisons were made of ova from both types, and of the aedeagii from the *I. patricia* holotype and *I. quinquepunctata* males from near the type locality.

   I. ebria (Hagen) is placed in synonymy with *I. sobria* (Hagen), based on similarity of the female genitalia and ova. Ova from both types were identical.

8. Keys based on comparative morphology are provided for all known males, females, ova, and nymphs of *Isoperla* and *Cascadoperla*.

9. Twenty-eight plates and 215 original illustrations, including SEM photographs, are presented.

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PART III

CHAPTER I

INTRODUCTION

Drumming behavior in stoneflies was first reported by Newport in 1851. A few qualitative descriptions of this unique behavior then appeared in the literature until 1966 (Briggs 1897, MacNamara 1926, Brinck 1949, 1956, Jewett 1959, and Gaufin et al. 1966). Needham and Christenson (1927) referred to Acroneuria pacifica as the "Western Drummer," and stated that the male drummed, using the "round percussion disc or hammer" on the 9th sternum to tap the substrate and attract the female.

Not until recent works by Rupprecht (1967, 1969, 1972, 1976), Gnatzy and Rupprecht (1972), Rupprecht and Gnatzy (1974), and Ziegler and Stewart (1977), was drumming quantified. Ziegler and Stewart (1977) characterized the drumming signals of 11 Nearctic stoneflies, representing the families Pteronarcyidae, Perlodidae, Perlidae, and Leuctridae, from Texas and Colorado, and analyzed signal lengths, number of beats, inter-beat intervals, and temperature variations.

Most stoneflies drum by striking the substrate with the terminal ventral part of the abdomen, but Rupprecht (presented paper, VI International Plecoptera Symposium, Schlitz, West Germany, Aug., 1977) has demonstrated that certain species of European Plecoptera drum by vibrating their abdomen at very high frequencies, without touching the substrate, and thus signals are transmitted through the air. Generally, males continue to drum during their entire life as an adult, but only virgin females respond to male signals. In most cases the female remains stationary throughout drumming communication, while the male actively searches, but in one species, *Isoperla grammatic* Poda, females also search (Rupprecht 1967).

Ziegler and Stewart (1977) reported that males always initiated the communication, females of some then answered, and in *Pteronarcella badia* (Hagen), *Hesperoperla pacifica* (Banks), *Claassenia sabulosa* (Banks), and *Pteronarcys californica* (Newport), males answered the females. Communication was therefore 2-way or 3-way.

There are no published reports of drumming behavior in Nearctic *Isoperla*. The purposes of this study were: (1) to analyze and describe the drumming signals of available western species, (2) to study species specificity, geographic variation, and relationships between distinct morphological species complexes, and (3) to provide additional input for my planned phylogenetic revision at the family level.

CHAPTER II

MATERIALS AND METHODS

The drumming signals of 4 *Isoperla* species (*I. phalerata* (Banks), *I. mormona* Banks, *I. fulva* Claassen, and *I. quinquepunctata* (Banks)), representing 3 distinct morphological species complexes within the genus *Isoperla*, were successfully recorded from 14 different western localities. Males and/or females of 3 species. *Isoperla rainiera* Jewett, *Isoperla marmorata* (Needham and Claassen), and *Cascadoperla trictura* Hoppe, were observed, but none were seen drumming. In all experiments, virgin adults were reared and correlated in the laboratory from late-instar nymphs, collected in Colorado, New Mexico, Oregon, and Washington, and maintained in 6-pac styrofoam containers in environmental chambers. Individuals were removed as they emerged, and held individually in shell vials in the chambers.

Temperature and light conditions in the laboratory during recording were monitored, using a Kahl Model 268WA620 light meter, and a hand-held thermometer. Recording of the drumming signals was done in a manner similar to that described by Ziegler and Stewart (1977) and consisted of: (1) a drumming chamber constructed from 8 X 5 note cards, (2) a Sony^{R} ECM-955 Electret condensor microphone, and (3) a Sony^{R} Model TC-142 cassette tape recorder and Ampex^{R} high fidelity 60 minute tapes. The drumming chamber was a 11 X 7 X 3 cm divided box, covered by a 14 mm dia. transparent plastic petri plate cover. The microphone rest 3 mm below the chamber, which was supported on 2 4-cm high foam rubber pads.

The cassette-taped signal recordings were played into a Tektronix 5115 Storage oscilloscope, and stored for measurement and photographing. The oscilloscope photographs were made with a Tektronix C-5A oscilloscope camera and Polaroid^R Type 107 ASA 3000 black and white film.

Important parameters analyzed were: (1) number of beats per signal, (2) signal length, (3) inter-beat frequencies, (4) interval between the first beat of the male signal and the start of the female response, (5) interval between the last beat of the male signal and the start of the female response, and (6) the number of male beats preceding the female signal. Specificity of all 4 species was tested by playing taped male signals of each species to groups of live females, and also by observing males and females of different species in all possible combinations in the drumming chamber. Geographic variation was tested by playing recorded signals of males from all collecting localities to the females.

CHAPTER III

RESULTS AND DISCUSSION

I. phalerata.-- Males exhibited a diphasic signal, which consisted of 2 separate phases with different numbers of beats, inter-beat frequencies, and signal durations. Range and $\bar{x}$ number of beats/1st phase of the male signal were 11-15 and 13.1 $\pm$ .9, respectively (Fig. 1, Table 1). Only one 11-beat and one 15-beat signal were recorded. Inter-beat frequencies remained constant throughout the first phase at 24.6 $\pm$ 3.7 ms. Range and $\bar{x}$ signal duration of the male first phase were 325-430 ms and 381.7 $\pm$ 39.4 ms, respectively. Range of the number of beats/2nd phase of the male signal was 14-26, and the $\bar{x}$ was 22.1 $\pm$ 3.7. Only one 14-beat and two 26-beat signals were recorded. Inter-beat frequencies remained constant throught the 2nd phase at 6.4 $\pm$ 1.2 ms, therefore much shorter than those of the 1st phase. Range and $\bar{x}$ of the duration of the male signal were 504-776 ms and 657.7 $\pm$ 67.7 ms, respectively.

The female signal was monophasic, ranging from 6-12 and having a $\bar{x}$ of 7.9 $\pm$ 1.7 beats. Only two 12-beat signals were observed. Inter-beat frequencies were fairly consistent throughout the signal at 27.1 $\pm$ 6.2 ms (Fig. 1, Table 1). Signal duration was quite variable, with a range and $\bar{x}$ of

Plate I, Figs. 1-6. Oscillographs of *Isoperla* (Plecoptera) drumming signals. 1. *I. phalerata* male and female signal. 2. *I. quinquepunctata* male and female signal. 3. *I. quinquepunctata* blending of male and female signals after an intense drumming period. 4. *I. quinquepunctata* female signal. 5. *I. mormona* male signal. 6. *I. fulva* male and female signal.

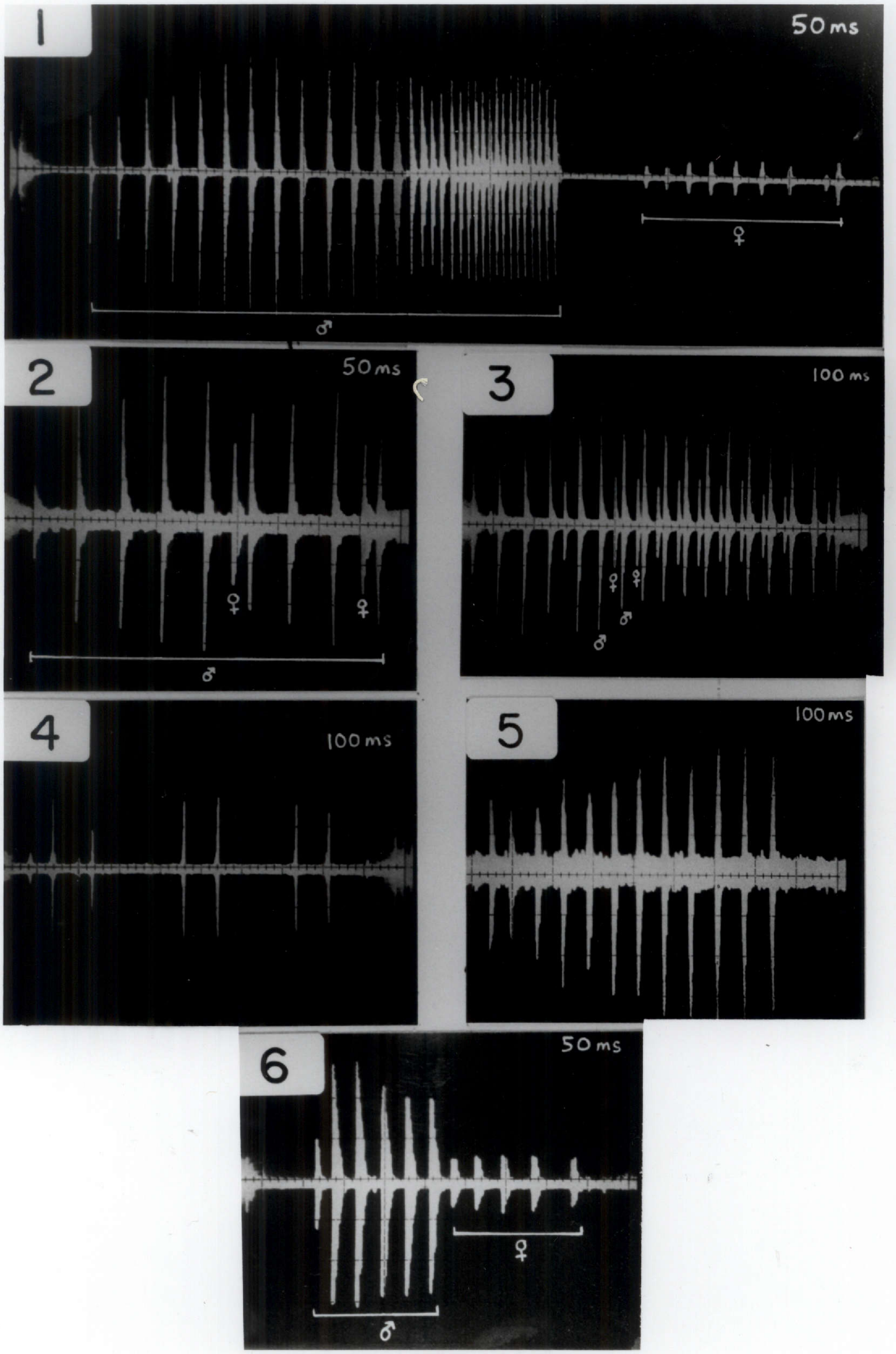
1
50ms
♀
♂
2
50ms
♀
♀
♂
3
100ms
♀
♀
♂
♂
4
100ms
5
100ms
6
50ms
♀
♂

Table 1. Drumming characteristics of *I. phalerata*, *I. quinquepunctata*, *I. mormona*, and *I. fulva*.

Species[1] / Localities / Temp. °C / Foot candles	No. Signals / No. Individuals ♂	No. Signals / No. Individuals ♀	Mode No. of beats/signal x̄ ± SD 1st phase ♂	Mode No. of beats/signal x̄ ± SD 2nd phase ♂	Mode No. of beats/signal x̄ ± SD ♀	Signal Length in ms x̄/ ± SD 1st phase ♂	Signal Length in ms x̄/ ± SD 2nd phase ♂	Signal Length in ms ♀	Interbeat Freq. in ms x̄/ ± SD 1st phase ♂	Interbeat Freq. in ms x̄/ ± SD 2nd phase ♂	Interbeat Freq. in ms ♀
I. phalerata											
(3)4♂2♀ (8)2♂2♀											
23 ± 1°C / 79 ± 1FC	298 / 6	139 / 2	13 / 13·1 ± ·9	22 / 22·1 ± 3·7	8 / 7·9 ± 1·7	381·7 / ± 39·4	229·6 / ± 154·2	251·6 / ± 44·7	24·6 / ± 3·7	6·4 / ± 1·2	27·1 / ± 6·2
I. 5-punctata											
(1)2♂ (2)5♂ (3)1♂											
2♀ (5)4♂3♀ (6)3♂											
(7)2♂ (8)2♂ (12)3♂											
3♀ (14)2♂											
22 ± 1°C / 80 ± 1FC	502 / 23	161 / 7	9 / 9·2 ± 2·8	—	2 / 2·1 ± 2·6	420·4 / ± 104·9	—	208·6 / ± 4·3	43·3 / ± 5·3	—	214·2 / ± 3·9
I. mormona											
(4)2♂											
23 ± 1°C / 80 ± 1FC	58 / 2	—	12 / 11·5 ± 5·3	—	—	641 / ± 161	—	—	45·9 / ± 9·3	—	—
I. fulva											
(2)6♂ (5)2♂ (7)1♂											
(9)1♂ (10)2♂3♀											
(13)4♂											
22 ± 1°C / 80 ± 1FC	352 / 10	63 / 2	6 / 5·6 ± ·5	—	5 / 5·3 ± 3·8	160·4 / ± 14·2	—	124 / 24·4	25·9 / ± 4·2	—	16·3 / ± 4·7

TABLE 2

Collection localities of _Isoperla_ reared for drumming experiments (number-referenced from Table 1)

(1) Colorado, Huerfano Co., Hwy. 160, 2 mi. W. of La Veta Pass, small crk. 6/V/1976 S. W. Szczytko and K. W. Stewart

(2) Colorado, Rio Blanco Co., Hwy. 5, 3.5 mi. S. of Hwy. 164, Piceance Crk. 25/V/1977 S. W. Szczytko and K. W. Stewart

(3) New Mexico, Rio Arriba Co., Hwy. 64, 15 mi. N.W. of Tres Piedras, small crk. 7/V/1976 S. W. Szczytko and K. W. Stewart

(4) Utah, Piute Co., Hwy. 89, N. of Big Rock Candy Mt. Sevier R. at bridge 2/VI/1977 S. W. Szczytko and K. W. Stewart

(5) New Mexico, Taos Co., below Palo Flechado Pass, small crk. at base of La Jara Canyon, Hwy. 64 8/V/1976 S. W. Szczytko and K. W. Stewart

(6) New Mexico, Colfax Co., Cimmaron Canyon 8 mi. W. of Ute Park Hwy. 64, small crk. 8/V/1976 S. W. Szczytko and K. W. Stewart

(7) Colorado, Jackson Co., Hwy. 125 N. of Walden, Michigan R. 9/V/1976 S. W. Szczytko and K. W. Stewart

(8) Colorado, Jackson Co., Hwy. 14 just N. of junct. Hwy. 40, S.W. of Walden, Grizzly Crk. 9/V/1976 S. W. Szczytko and K. W. Stewart

(9) Colorado, Eagle Co., Hwy. 131, below McCoy, Rock Crk. 10/V/1976 S. W. Szczytko and K. W. Stewart

(10) Colorado, Dolores Co., Hwy. 145, below Lizzard Head Pass, N. of Rico, Upper Dolores R. 11/V/1976 S. W. Szczytko and K. W. Stewart

(11) Utah, San Juan Co., Hwy. 160 S. of Moab, Manti La Sal National Forest, Pack Crk. 11/V/1976 S. W. Szczytko and K. W. Stewart

(12) Utah, Millard Co., off Hwy. 15, above the town of Kanosh, small crk. in Kanosh Canyon 1/VI/1977 S. W. Szczytko and K. W. Stewart

TABLE 2 (con't)

(13) Utah, Salt Lake Co., Butterfield Canyon Crk. 1st canyon S. of the town of Lark 13/V/1976 S. W. Szczytko and K. W. Stewart

(14) Utah, Duchesne Co., Hwy. 40 in town of Duchesne, Duchesne R. 14/V/1976 S. W. Szczytko and K. W. Stewart

192-356 ms and 251.6 $\pm$ 44.7 ms, respectively. The range of the time interval between the first beat of the male signal and the beginning of the female response was 620-825 ms, and the $\bar{x}$ was 689 $\pm$ 75.5 ms. The range and $\bar{x}$ durations between the last beat of the male signal and the beginning of the female response were more stable at 80-135 ms and 90.8 $\pm$ 10.5 ms, respectively. Drumming in this species was therefore a triphasic 2-way communication.

Male and female *I. phalerata* required no inducement to initiate drumming, and they drummed quite frequently under laboratory conditions. All recordings were made between 22-24° C and 78-80 fc. In almost every case, the female answered every male signal. During the communication the male actively searched, stopping periodically to drum, while the female remained stationary.

The amplitude of the male signal remained relatively the same throughout the first and second phases, but was always much greater than the female signal, which was constant. Females never responded until the male signal was completed. Also, they did not respond to male signals of *I. fulva*, *I. quinquepunctata*, or *I. mormona*.

I. quinquepunctata.-- Males and females of this species exhibited monophasic signals and 2-way communication. Range and $\bar{x}$ number of beats/male signal were 3-17 and 9.2 $\pm$ 2.8, respectively (Fig. 2, Table 1). Inter-beat frequencies were fairly constant at 43.3 $\pm$ 5.3 ms. Duration of the male signal varied considerably, with a range of 236-832 ms, and a $\bar{x}$ of 420.4 $\pm$ 104.9 ms.

Range and $\bar{x}$ number of beats/female signal were 1-4 and 2.1 $\pm$ 2.6. Total duration of the mode, 2-beat signal had a range of 46-287 ms and a $\bar{x}$ of 208.6 $\pm$ 4.3 ms. The time interval between the first beat of the male signal and the start of the female signal was relatively constant, with a range of 248-296 ms and $\bar{x}$ of 250.8 $\pm$ 7.9 ms. The female response usually came after the male 6th beat, and exhibited a range and $\bar{x}$ of 5-8 and 6.1 $\pm$ 1.6 ms, respectively. Females always answered before completion of the male signal, and therefore there was no time interval between the last beat of the male signal and the start of the female signal.

This species demonstrated the greatest amount of variability of the 4 studied. Males did not require any stimulus in the laboratory to initiate drumming, and most individuals drummed quite frequently, if not constantly, as can be observed by the large number of recorded signals (Table 1). Recordings were made between 21-23^{o} C and 79-81 fc. After one male began to drum, all other males and females exposed to the signal responded. In nature, this would result in a "natural streamside symphony" of combined and overlapped signals. During this synphony, male and female signals overlapped, and in many cases the male signals became aborted. After a period of intense drumming activity by a number of males and females, the number of beats/male signal became very inconsistent, and females would answer almost every beat of the male (Fig. 3). There was also a general trend for the number of beats and signal duration of the male to decrease steadily, from the mode number of 9 beats to 3 or 4, and from a $\bar{x}$ signal length of 420.4 ms to 110 ms. In many cases, males were so active during this period that they would start another drumming sequence before stopping to the usual fixed position. This undoubtedly contributed to aborted signals, due to loss of footing, and aberrated upside-down positioning. Also during symphonies, one female was observed drumming after normal 2-way communication was completed, and in several instances she initiated drumming from the male by repeating a series of 3, typical 2-beat signals (Fig. 4).

Females from Butterfield Canyon, Salt Lake Co., Utah, placed in a drumming chamber with I. mormona males from the Sevier R., Piute Co., Utah, responded to the male signals after the 5th or 6th beat. The inter-beat frequencies of male I. mormona and I. quinquepunctata signals were very similar, 43.5 $\pm$ 5.3 ms and 45.9 $\pm$ 9.3 ms, respectively (Table 1); however, the length of the signals and number of beats were different. The closeness of the inter-beat frequencies explain the female response after the 5th or 6th beat, and is very similar to the situation described for Perlinella drymo (Newman) females, and Pteronarcella *badia* (Hagen) males, by Ziegler and Stewart (1977). The females continued to answer all male signals throughout the experiment, and upon placing the male and female together, males attempted to mount and mate. However, females exhibited an avoidance response by raising the abdomen and fluttering the wings to prevent copulation, similar to that described by non-virgin females of *Capnia bifrons* Newman, *Isoperla grammatica* Poda, *Dinocras cephalotes* Curtis, and *Perla marginata* Panzer by Rupprecht (1967). The general body size of *I. quinquepunctata* females was approximately 4-5 mm greater than *I. mormona* females. This and other isolating mechanisms probably prevent hybridization in sympatric populations.

I. quinquepunctata females did not respond to male signals of *I. fulva* or *I. phalerata*, although they would answer to the tapping of a pencil approximating the typical number of beats and inter-beat frequency of the male. During the experiments, females remained stationary while males actively searched, stopping occasionally to drum.

The amplitude of the male signals remained constant throughout, and was always greater than the female.

I. mormona.-- Males exhibited a monophasic signal. Range and $\bar{x}$ number of beats were 6-16 and 11.5 $\pm$ 5.3, respectively (Fig. 5, Table 1). The inter-beat frequency was fairly consistent at 45.9 $\pm$ 9.3 ms. The range of the signal duration was 375-1152 ms, and the $\bar{x}$ was 641 $\pm$ 161 ms. Amplitude of the male signal increased slightly from the beginning to the end of the signal. Recordings were made between 22-24^{o} C and 79-81 fc.

Males would not drum until 2 days after emergence. Inducement was often required for initiation of their signals. This was accomplished by gently tapping with a pencil, producing a long series of evenly spaced beats on the table top, or by playing a previously recorded signal. After drumming once, the males usually then continued to drum on their own. Signals were obtained from only 2 of the 9 males reared.

Eight females, which emerged along with the males, were observed for one week; one drummed only twice, but would not repeat while in the recording chamber. It appeared that the signals were monophasic and consisted of 3-5 beats after the completion of the male signal, but analysis was precluded because signals were never successfully recorded.

I. fulva.-- Males exhibited a monophasic signal. Range and $\bar{x}$ number of beats were 5-6 and 5.6 $\pm$ .5, respectively (Fig. 6, Table 1). Inter-beat frequencies were relatively constant at 25.9 $\pm$ 4.2 ms. Signal duration ranged from 104-198 ms, and the $\bar{x}$ was 160.4 $\pm$ 14.2 ms.

The female signal was also monophasic; range and $\bar{x}$ number of beats were 3-6 and 5.3 $\pm$ 3.8, respectively. Inter-beat frequencies remained constant throughout the signal at 16.3 $\pm$ 4.7 ms. Signal duration of the mode, 5-beat signal ranged 96-188 ms with a $\bar{x}$ of 124.4 $\pm$ 24.4 ms. The range and $\bar{x}$ for the time interval between the first beat of the male signal and the start of the female signal were 94-172 ms and 11-.4 $\pm$ 19.2 ms, respectively. The range for the time interval between the last beat of the male signal and the start of the female signal was 10-40 ms, and the $\bar{x}$ was 13.5 $\pm$ 8.5 ms. Communication between the male and female was 2-way. All recordings were made between 21-23^{o} C and 80 fc.

Drumming activity required no inducement, and most individuals drummed quite frequently, as indicated by the number of signals analyzed (Table 1). During drumming, males remained stationary until receiving a response from the female, whereupon they became very excited and actively searched for the female. Throughout this searching they would only stop briefly to drum, and in several cases gave a number of shortened, aborted signals of 3-4 beats.

In all recorded signals, females always answered after the completion of the male signal. Generally, the amplitude of the male signal decreased slightly throughout its length, but was always much greater than that of the female. Amplitude of the female signal was usually constant.

I. rainiera.-- Three lab-reared males and 2 reared females, collected from a small stream on Mt. Hood, Clackamas Co., Oregon, were studied, and drumming was not observed. Females did not respond to signals of *I. fulva*, *I. phalerata*, *I. mormona*, or *I. quinquepunctata*.

I. marmorata.-- One lab-reared female from the Upper Wynoochie R., Grays Harbor Co., Washington, did not answer signals of *I. fulva*, *I. phalerata*, *I. quinquepunctata*, or *I. mormona*. No live males were reared. From a concurrent morphological study, it is apparent that *I. fulva* and *I. marmorata* represent a two-species complex which is morphologically very homogenous. Since *I. marmorata* females did not answer male signals from *I. fulva*, this would indicate that the signals in this complex are probably species-specific.

Cascadoperla trictura.-- Four field-collected males, 3 lab-reared males, and 4 reared females, taken from the Alsea R., Benton Co., Oregon, were observed, and no indication of drumming was seen or recorded.

An experiment was conducted to reflect on the usefulness of drumming as a premating locating device for males and females that might emerge in a natural situation along the stream margin, and drum on large boulders where there is an abundance of extraneous noises, including rushing water, to interfere with signal transmission and reception. A loud, roaring riffle was recorded from Clear Crk., Sevier Co., Utah. Males and females of *I. quinquepunctata*, collected from a small stream in Kanosh Canyon, Millard Co., Utah, were reared in the laboratory and placed in separate drumming chambers. Each chamber was insulated from a table top by a foam rubber pad, and place approximately

6 feet apart on separate, heavy tables. Male drumming was induced by playing a previously recorded taped male signal. After drumming was initiated, the tape recording of the stream riffle was played at full volume, approximating the level of noise at stream side. This recording, plus the noise of exhaust fans and other extraneous sounds in the laboratory, provided an array of different vibrations and sound frequencies. Females answered the males repeatedly through this screen of noises, and the foam pads precluded the probability that signal vibrations were being transmitted via the substrate (tables and floors). It was clearly observed that the female only drummed just prior to the completion of the male signal, as was typical under quiet conditions. It would seem, therefore, from the results that these insects must have the ability to filter out extraneous sound frequencies, and are "tuned" to the proper signal characteristics. This would be very important in the effectiveness of drumming as a locating and isolating mechanism for species in their natural surroundings.

I feel that the antennae generally serve as signal receptors, since they remain deflected down on the substrate during drumming communication. The sensory hairs, plentiful along the length of the antennae, and other body parts are probably the specific receptors. These suppositions need additional testing.

CHAPTER IV

GENERAL DISCUSSION

From a concurrent morphological study, it is apparent that the 6 species of *Isoperla*, and one *Cascadoperla* studied, represented 4 species complexes within the genus *Isoperla*, and a monotypic complex of the new genus *Cascadoperla* that I have just described. Three of these *Isoperla* species complexes were represented by recorded signals. All exhibited substantive differences in the number of beats, signal duration, and inter-beat frequencies in both males and females. Inter-beat frequency was the most consistent parameter in each species. In all groups drumming was a simple, 2-way communication. All males studied possessed a "hammer" or vesicle on the 8th sternum which they used to strike the substrate during drumming.

I. phalerata represented a 2-species complex which included *I. pinta* Frison. Their signals were very different from the others studied, because the male signal was diaphasic, and the female signal contained more beats than those representing the other 2 groups.

I. quinquepunctata and *I. mormona* represented a 4-species complex, which also includes *I. longiseta* Banks and *I. jewetti* Szczytko and Stewart. Males of both exhibited a rather long monophasic signal, and females had few beats. _I_. _quinquepunctata_ females were unique, in that they responded before the completion of the male signal. _I_. _mormona_ females, however, appeared to answer after the completion of the male signal. The similarities between the drumming signals within this complex can be seen by comparing the closeness of the male inter-beat frequencies (Table 1), and by the fact that females of _I_. _quinquepunctata_ responded to the male signals of _I_. _mormona_ after the 5th or 6th beat, further emphasizing the importance of signal frequencies in species (or group) specificity.

_I_. _fulva_ and _I_. _marmorata_ represented a third 2-species complex. Male and female signals were monophasic and differed from the other 2 mentioned groups in the few beats of male signals and the shorter inter-beat intervals of both male and female signals.

The morphological separation of _Isoperla_ species complexes generated by my concurrent study was supported by the distinctiveness of signal parameters for each of these 3 complexes. The fact that no female would answer males from another complex, and the similarities between signals within a complex, further solidifies my contention that drumming will prove to be very valuable, quantifiable input in considering phylogeny among the Plecoptera. This possibility was first suggested by Zwick (1973).

All species studied were sympatric, and no distinct geographic variations or clines were found. It was apparent that there was as much internal variation within a population, and even within one individual, as there was between populations. The consistencies of the inter-beat frequencies, and the fact that females of a given species would respond to signals of the same species from different localities, indicates that dialects, at least among these Isoperla species, are either non-existent or are of little functional significance.

The greatest variation was noted in signal lengths, which was directly related to the number of beats. It was realized from visual observations that some of the male signals were actually aborted due to unfixed or aberrated positioning just prior to the start of drumming, drumming upside-down on the petri plate cover, and drumming during extended periods of intense communication between males and females. In general, signal length of the female exhibited less variation than the male, and was probably due to her inactivity and lack of movement during drumming. For these reasons, the value of statistical treatment of data would have meaning only if positions and footing of males is recorded with each signal.

Future use of drumming behavior for additional input in constructing phylogenetic schemes, and for use in support of classical morphological studies, should prove to be invaluable, based on the findings of this study.

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