THE STONEFLY GENUS *Isogenoides* KLAPÁLEK (PLECOPTERA: PERLODIDAE) OF NORTH AMERICA: SYSTEMATICS, BEHAVIOR AND ECOLOGY

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The stonefly genus *Isogenoides* is revised following a holomorphological approach utilizing traditional morphology and behavioral lines of evidence. Species keys are provided for all life stages. One species, *I. krumholzi* (Ricker) is considered a synonym of *I. doratus* (Frison). Detailed species descriptions are provided for males, females, nymphs and ova. Distributions are updated utilizing all known published accounts and materials examined.

The vibrational communication (drumming) behavior is reported for males and all but one species for females. The signals were species-specific and ranged in complexity from ancestral sequenced duets to derived grouped exchanges. *Isogenoides olivaceus* is least specialized, having mostly sequenced duets, and *I. zionensis* most specialized, displaying ancestral sequenced, derived grouped and complex derived exchanges containing both sequenced and grouped elements.

Laboratory egg incubation experiments over a 2–4 year period show that *Isogenoides* has a great capacity for extended, sometimes-asynchronous diapause and hatching. The eggs of six species were incubated at a single, ca. simulated San Miguel River, Colorado, seasonal temperature regime. Direct hatch within two weeks occurred only for *I. zionensis* (Leopard Creek, Colorado) with small numbers hatching again after one, two, and four years. Eggs of *I. doratus* and *I. varians* hatched after an over summer, 3–5 month diapause, and *I. varians* again in August the next year. Populations of *I. colubrinus*, *I. elongatus*, *I. frontalis* and San Miguel River, *I. zionensis*

began hatching after a 9–11 month diapause and again during spring-summer temperatures in 2nd through 4th years.

Isogenoides zionensis in the San Miguel River, Colorado, exhibited a semivoltine life cycle over the two-year study period. Adults emerged in June-July when stream temperature reached ca. 11–17°C. Reared females at Quartz Creek, Pitkin, Colorado, deposited up to three egg batches. Mean fecundity of females was 691 egg/female. Oviposition in the field was observed and described.

Nymphal growth was exponential from June to December, followed by slow growth until April, then declined until emergence. The greatest growth occurred between July and December as stream temperature decreased to minimum and maximum size was obtained in March while stream temperature began to increase.

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PREFACE

This research on the stonefly (Plecoptera) genus *Isogenoides* was begun in December 1999. The overall objective was to rear fresh material of all the species from type or other historical and new localities, and use it along with all known personal and museum collections for comparative study of all the life stages to add substantially to the then-limited knowledge about the genus.

Major systematics and biological questions needing clarification or new knowledge were: 1. Interspecific differences and intraspecific variation of adult genitalia, pigment patterns and other characters. 2. Comparative descriptions of the eggs of all species. 3. Comparative descriptions of the larvae of all species. 4. Intersexual communication (drumming) signals and behavior of all species. 5. A thorough, baseline life history of at least one species. 6. Capacity for extended diapause in eggs of species. 7. Preliminary assessment of the potential use of DNA to help clarify species delineation and phylogeny within the genus, and as a contribution to phylogenetic analysis of Plecoptera, and 8. Clarification of the status of previous synonymies of the problematic species *Isogenoides hudsonicus* with *I. frontalis* and *I. colubrinus* with *I. frontalis*. These therefore became the specific objectives of the research.

Over the five years of study, collecting expeditions were made, with the help of several workers listed in the acknowledgements, to type and other localities in Colorado, Iowa, Michigan, Mississippi, Virginia, West Virginia and Wisconsin. Successful rearing, leading to fresh study material of all life stages and drumming recordings, were obtained from most of these explorations, and the comparative study of the species using traditional light microscopy, scanning electron microscopy, audio

and video recordings and analysis of drumming using updated technology, long-term-holding of live eggs in a laboratory stream for diapause determinations, and collaborative study with personnel of Brigham Young University in isolation and description of DNA markers was accomplished. In addition, a detailed study of the life history of *I. zionensis* was conducted on a San Miguel River, Colorado, population in 1999-2001.

My presentation is divided into the following chapters: 1. General introduction, 2. Holomorphology and systematics, 3. Drumming signals and behaviors, 4. Capacity for extended egg diapause and 5. Life history of a San Miguel River, Colorado, population of the widespread western species *I. zionensis*. Data on *Isogenoides* DNA, from specimens I collected during this study are currently included in a manuscript in preparation by senior author Matthew Terry, formerly of Brigham Young University, and therefore is not included in this dissertation.

CHAPTER 1

GENERAL INTRODUCTION

Stoneflies (Plecoptera) are a relatively small order of hemimetabolous aquatic insects with over 2,100 species world wide (McCafferty et al. 1990), and 628 recognized from America north of Mexico (Stark 2001b). They are an important insect order in stream ecosystems, forming an integral component of food webs. The nymphs are generally considered to be intolerant of anthropogenic activities, and therefore good indicators of water quality (Baumann 1979; Rosenberg and Resh 1993). Plecoptera are excellent organisms for the study of biogeography and evolution because of their low vagility, the manageable size and diversity of the group, and the multiple life stages and unique behaviors from which data may be collected (Stewart and Stark 1988, 2002).

Almost all adult stoneflies are terrestrial, living in streamside and riparian habitats, and cryptic so that they are seldom encountered except by those actively searching for them. Their life spans are ephemeral, ranging from about 1-4 weeks. Adults of the suborder Arctoperlaria have adopted a complex vibrational communication system, where both sexes produce species-specific vibrational signals by drumming or rubbing their abdomens against the substrate, or by rocking or vibrating their whole bodies (tremulation); these vibrational duets aid calling males in finding answering females (Alexander and Stewart 1997, Stewart 1997, 2001).

Nymphs are aquatic, with most species inhabiting running water in a variety of habitats from spring seeps to streams and rivers. The majority of species occur in cool, highly oxygenated and relatively non-polluted lotic systems, but a few occur in turbid, warm or intermittent streams. A small number of species occur in cold arctic or alpine

lakes, or moving water situations of more southern latitude lakes. Nymphs of the group Euholognatha are generally herbivorous (shredders), and those of the group Systellognatha insectivorous (engulfers of various invertebrate groups), but some species have ontogenic shifts in their food habits, where early instars are herbivore-detritivores, middle instars are omnivores, and late instars become exclusively insectivores (Fuller and Stewart 1977, Stewart and Stark 2002).

The first comprehensive study of the North American fauna was by Needham & Claassen (1925), and Claassen (1931) wrote the first treatise on nymphs. World catalogs were published by Claassen (1940), Illies (1966) and Zwick (1973). The Illies catalog gave a-priori generic status to previously proposed subgenera by Ricker (1943, 1952) and others; this profoundly affected stonefly systematics by substantially increasing the number of genera. A rigorous morphological study and phylogenetic analysis was done by Zwick (1973, 1980), who proposed the currently recognized suborders Arctoperlaria and Antarctoperlaria and the arctoperlarian groups Euholognatha and Systellognatha.

Plecoptera species have been delineated by external and internal male genitalia, and to lesser extent female genitalia, and eggs. Definition of systellognathan species in genera with cryptic (sibling) species, where the external male genitalia are homogeneous, have required additional characters such as the male aedeagus and internal female characters; examples: *Neoperla* (Stark and Baumann 1978, Ernst et al. 1986, Stark 1990), *Acroneuria* (Stark and Gaufin 1976), *Isoperla* (Szczytko and Stewart 1979), *Perlesta* (Stark 1989), Suwallini (Alexander and Stewart 1999), and more recently the large, mostly neotropical genus *Anacroneuria* (Stark 1995, 1998, 1999,

2000, 2001a, Stark and Kondratieff 2004, Stark and Sivec 1998, 2001, Stark and Zúñiga 2003, Stark et al. 1999, 2001). Furthermore, stonefly researchers have increasingly realized that a more holistic approach to systematics would lead to the best definition of species, genera and phylogenetic inferences. Such an approach would utilize these additional genitalic characters and other morphological characters (Hennig's 1966 "holomorphology") and additional lines of available evidence such as behavioral, genetic, biochemical, physiological and ecological, as proposed by Ross (1974).

The utilization of additional suites of characters beyond external morphology in stoneflies has been mainly to use internal genitalia characters (Alexander and Stewart 1999, Ernst et al. 1986, Stark and Baumann 1978, Stark and Gaufin 1976, Stark et al. 1999, and Szczytko and Stewart 1979), eggs (Stark and Szczytko 1984, 1988), nymph characters (Poulton and Stewart 1991, Stewart and Stark 2002, Szczytko and Stewart 1976, 1984, 2002, 2004), drumming and mate-searching behaviors (Alexander and Stewart 1996a, 1996b, Maketon et al. 1988, Stewart 1997, 2001, Stewart and Maketon 1990, Stewart and Zeigler 1984, Stewart et al. 1982, Stewart et al. 1988, Zeigler and Stewart 1987). Only a few workers have utilized any one or few of these character categories for even one or two genera, and none have utilized the full spectrum of categories for any genus.

My comparative approach in this study involved the examination of several lines of evidence, including morphological, behavioral, and genetic characters (Table 1). These lines will be incorporated into the results in this and following chapters of this dissertation, and a matrix of observed characters is presented in the Appendix.

I chose the genus *Isogenoides* because of its potential to serve as a model for holistic study using multiple lines of evidence, and my interest in the family Perlodidae. The genus offered an excellent possibility for all the requisites necessary to serve as such a model, because: 1. It was a well-defined group by the mesosternal ridge pattern of nymphs and adults, 2. It was of a workable size of nine species with reasonable expectations that fresh material of all life stages could be reared for morphological, behavioral, genetic and ecological studies, 3. Distribution and adult presence times were reasonably well known, that would facilitate biological study in the field, and 4. The limited knowledge of drumming of only two species, *I. zionensis* Hanson and *I. elongatus* (Hagen) (Stewart and Zeigler 1984, Zeigler and Stewart 1987) suggested a fruitful pursuit of quantifiable, species-specific behavioral data.

Our knowledge of the life histories and ecology of North American *Isogenoides* species was very meager; there had been no definitive, comprehensive study published of the life history of any species. A partial life history of *I. zionensis* from the Rio Conejos, Colorado, was published by DeWalt and Stewart (1995). A study of nymphal growth for *I. frontalis* (Newman) and *I. olivaceus* (Walker) had been conducted in the northern Lower Peninsula of Michigan (Haro et al. 1994). It was also known that emerging adults take refuge in streamside debris or crawl or fly into riparian woody vegetation or to the tree canopy encounter sites as bushtoppers or treetoppers (Stewart 1994).

Nymphal species descriptions were incomplete, except for that of *I. zionensis* (Baumann 1973) and *I. colubrinus* (Hagen) (as *I. zionensis*, Stewart and Stark 2002). The nymph and adult female of *I. krumholzi* (Ricker 1952) were undescribed and the

nymph of *I. doratus* (Frison) was described in the genus *Hydroperla* from an exuvium of a laboratory-reared adult (Frison 1942). Some details of the nymph of *I. colubrinus* were briefly described by Claassen (1931), however the specimen had no collection label, leaving doubt as to its actual identity. Frison (1937, 1942) and Ricker (1952) provided nymphal descriptions with varying levels of completeness that included the remaining five species: *I. elongatus*, *I. frontalis*, *I. hansoni* (Ricker), *I. olivaceus*, and *I. varians* (Walsh). Other than the distinct posterior abdominal character illustrated for *I. olivaceus*, these nymph descriptions were brief and lacked the necessary detail for comparative study or development of a species key. In some cases illustrations were not accompanied with a written description.

Adults were relatively well described with various supportive illustrations provided. However, they were brief, non-comprehensively comparative, and in some cases erroneous. An example was Frison's (1942) new species description of *I. doratus*. The adult male and female illustrations were actually of *I. hansoni* (INHS # 1553 – *I. doratus* paratype male from Brodhead Creek, Pennsylvania). The identity of the *I. doratus* Holotype male remained unknown for 10-years, until Hanson (1953) provided a complete description with illustrations of the male and female genitalia. Another example of past confusion was the status of *I. hudsonicus* (Hanson), a species that was synonymized with *I. frontalis* by Ricker (1944). The synonymy was based on three conclusions. First, an intermediate condition occurred between the two species in the shape of the major distinguishing character, genital lobes; secondly all other diagnostic characters were even more variable than the genital lobes; and thirdly all of the variations were attributable to latitude. The most complete species key to males

and females was provided by Ricker (1952) that included all currently recognized species except *I. zionensis*. Hanson (1943), Harden and Mickel (1952), Hitchcock (1974), and Baumann et al. (1977) all provided regional species keys.

Currently, the genus *Isogenoides* includes nine North American species. 1. *I. colubrinus* (Hagen 1874) 2. *I. doratus* (Frison 1942) 3. *I. elongatus* (Hagen 1874) 4. *I. frontalis* (Newman 1838) 5. *I. hansoni* (Ricker 1952) 6. *I. krumholzi* (Ricker 1952) 7. *I. olivaceus* (Walker 1852) 8. *I. varians* (Walsh 1862) 9. *I. zionensis* Hanson 1949. I propose in this study to reduce this to eight, by recognizing *I. krumholzi* (Ricker 1952) as a synonym with *I. doratus* (Frison 1942).

Table 1. Lines of evidence used to delineate Isogenoides species.

Lines of Evidence	Characters Examined
Adult ♂	Morphological: hemitergal lobe, external genitalia (epiproct characters and setation, lateral stylets).
Adult ♀	Morphological: external genitalia (subgenital plate), abdomen setation.
Ovum	Morphological: external chorion characters.
Nymph	Morphological: external characters and developing internal male reproductive structures.
Drumming Signals	Behavioral: # of beats, intervals between beats, # of groups of beats, intervals between groups, Total avg. intervals between all beats
DNA	Molecular: 18S rDNA Entire region and Cytochrome Oxidase II (COII)

CHAPTER 2

HOLOMORPHOLOGY AND SYSTEMATICS OF THE STONEFLY GENUS *Isogenoides* (PLECOPTERA: PERLODIDAE)

Introduction

Isogenoides is a genus of the North American stonefly family Perlodidae, originally established by Klapálek (1912) as a subgenus, split from *Isogenus* (Newman 1833). This subgeneric placement was continued by Claassen (1940). Since then, at least eight more North American genera have been split from *Isogenus* (Zwick 1973), leaving it currently defined as restricted to the western Palearctic region (Hanson 1943, Ricker 1952, Stewart and Stark 2002). *Isogenoides frontalis* (Newman) was designated type species for *Isogenus* by Klapálek (1912). The subgeneric designation was also continued by Ricker (1952), Hilsenhoff and Billmyer (1973) and other workers, despite Hanson's (1943) elevation to full generic status. Ricker (1952) gave descriptions and keys to seven species of adults, treating *I. frontalis* and *I. colubrinus* (Hagen) as subspecies of *frontalis*, and included anecdotal descriptions of six species of nymphs. Illies (1966) also supported Hanson's (1943) generic status of *Isogenoides* by his a-priori elevation of all stonefly subgenera to genera. Some *Isogenoides* species have been variously assigned to the genera *Isogenus* Newman (Needham and Claassen 1925, Frison 1942), *Hydroperla* Frison (Frison 1937, 1942) and *Perla* Geoffroy (Banks 1918, 1920).

The objectives of this research were to: 1. rear fresh material of all nine currently recognized *Isogenoides* species: *I. colubrinus*, *I. doratus* (Frison), *I. elongatus* (Hagen), *I. frontalis*, *I. hansoni* (Ricker), *I. krumholzi* (Ricker), *I. olivaceus* (Walker), *I. varians*

(Walsh), and *I. zionensis* Hanson, and 2. use the freshly reared specimens of all life stages, along with historical personal and museum collections, to prepare detailed comparative morphological descriptions, illustrations and keys for delineation of species.

Materials and Methods

In addition to extensive field collections and field and laboratory rearing, many *Isogenoides* specimens from all known university, museum and individual holdings, in addition to the University of North Texas entomological research collection, were examined. Cooperating individuals and their university affiliations that loaned or donated specimens included: Dr. R. W. Baumann and Dr. C. R. Nelson, Monte L. Bean Life Sciences Museum, Brigham Young University (BYU); Dr. B. C. Kondratieff, C. P. Gillette Museum of Arthropod Biodiversity, Colorado State University (CSU); E. Richard Hoebeke, Cornell University Insect Collection, Ithaca, NY (CUIC); Dr. P. P. Harper, University of Montreal (UM).

Curators, directors and staff of major institutional museums that loaned specimens or provided digital photographs were: W. J. Reynolds and M. G. Fitton, The British Natural History Museum, London, UK (BNHM); D. W. Webb, R. E. DeWalt and Kathleen Zeiders, Illinois Natural History Survey (INHS); P. D. Perkins, Museum of Comparative Zoology, Harvard Univ. (MCZ); O. S. Flint, Jr. and David Furth, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH).

In addition, the following individuals loaned specimens from their personal collections: B. P. Stark, Mississippi College, Clinton, MS (BP); D. Etnier, University of Tennessee, Knoxville, TN (DE); J. Earl, Pennsylvania Department of Environmental

Protection, Harrisburg, PA (JE); R. J. Haro, University of Wisconsin, La Crosse, WI (RH); D. H. Funk, Stroud Water Research Center, Avondale, PA (DF); W.E. Ricker, Nanaimo Research Station, Vancouver Island, BB. Abbreviations for collections of the authors are John B. Sandberg (JBS) and Dr. K. W. Stewart, University of North Texas (includes W.E. Ricker material) (UNT).

Collecting trips were made to Colorado and Michigan in April, May, and June, 1999, to coincide with emergences of *I. olivaceus, I. doratus*, *I. elongatus*, and *I. zionensis*. Collection trips in 2000 were made to, Mississippi Wisconsin, and Colorado to coincide with emergences of *I. varians* (February), I*. frontalis* (April), and *I. colubrinus* (May), respectively. In February 2001, a collecting trip was made to Virginia to coincide with the emergences of *I. hansoni* and a second population of *I. varians*. In February 2002, the Rock River in Northeastern Iowa was visited to collect mature nearly nymphs from a second population of *I. doratus*.

Pre-emergent nymphs were collected and transported live in foam 6-pack coolers (Szczytko and Stewart 1979) with stream water, and kept cold inside ice chests. Containers were checked daily, and correlated adults, exuviae and additional nymphs were preserved in both 75% ethyl alcohol (EtOH) and Kahles solution in an attempt to optimize pigment pattern retention. When returned to the lab, live nymphs were reared individually in perforated foam cups containing coarse gravel and partially suspended through holes in a floating foam sheet, in a Living Stream® controlled environment (Frigid Units Inc.®, Toledo, OH, http://www.frigidunits.com/). The Living Stream® was adjusted to a single simulated seasonal temperature regime determined by submerging a Ryan® temperature monitor Model RL100™ (Ryan® Instruments, Redmond, WA,

http://www.ryaninst.com/) in the San Miguel River, Colorado, for the period of July 1999 to July 2000. During that year, the laboratory stream was adjusted to periodic San Miguel River temperatures obtained from a thermometer during trips from Texas to Colorado for an associated study of *I. zionensis* life history. De-ionized water and Proper pH 7® water additive (Aquarium Pharmaceuticals, Inc., Chalfont, PA, http://www.aquaiumphar.com/) were used in the Living Stream®, and partial water replacements, measurements of pH, total alkalinity, and total hardness, were conducted monthly. In some cases, increasing the water temperature gradually enhanced emergences beyond expected periods. The diurnal photoperiod was periodically adjusted to appropriate field conditions.

Immature nymphs without black wing-pads required periodic feeding of small midge and mayfly larvae. The individual rearing cups were covered with plastic lids so newly emerged adults could be seen and transferred to dry holding chambers and used for an associated drumming study or preserved in reared series.

The epiproct (and to variable degrees, the lateral stylets) and membranous aedeagus of recently expired males were everted by squeezing the abdomen, using the thumb and forefinger of one hand to squeeze, and a cotton tipped wooden applicator in the other hand to push on the expanding ninth sternite. We modified the methods provided for this preparation by Szczytko and Stewart (1979), by conducting the above step under a dissection microscope at 0.8x magnification. Once the aedeagus was fully everted, a “soft-touch” thin forceps was used to keep it everted during fixing by firmly pinching the abdomen at the 5^{th} or 6^{th} segment, because if the abdomen were released, the epiproct and aedeagus would be withdrawn back into the abdomen. The specimen

was then placed into near-boiling deionized water for 3-5 seconds. This procedure "fixed" the everted positions of both the aedeagus and the epiproct, and is highly recommended to stonefly collectors, since clearing abdominal segments in solutions of Potassium Hydroxide (KOH) has caused folding of epiproct tissue, preventing clear observation of important characters. Before further dissection of the male reproductive structures (character terminology by Stark and Nelson 2000), digital photographs (Fig. 1) and tracings were obtained with ZEISS® intermediate phototube (Carl Zeiss Light Microscopy, Göttingen, Germany, http://www.zeiss.de/micro.com/), SONY® digital camera Model DSC-S85 (Sony Corporation, Tokyo, Japan, http://www.sony.net/SonyInfo/CorporateInfo.com/), and ZEISS® drawing apparatus, Model S. An illustration of the last 3 male segments was produced using either lateral or oblique-lateral views to illustrate reproductive structures of everted specimens.

The male epiproct, lateral stylets and internal basal anchor (structure joined to the base of epiproct internally, attached by dorsal wing-like sclerites near the anterior margins of the 10^{th} tergite, and anterior to the epiproct) were removed from the abdomen to be prepared for SEM study. This was accomplished using "minuten" tipped probes and extremely fine forceps to remove internal muscular and external connective membranous tissues from the various sclerotized structures. If needed, short baths in strong >50 percent, heated or unheated KOH solutions helped remove remnant tissues that might obscure clear study using SEM. The adult female subgenital plate (abdominal sternite 8) was also dissected and prepared using the above method.

Sclerotized reproductive structures and mature ova were then prepared for SEM by the following method: 1. Structures and eggs were sonicated in either glass

microvials (12 mm long x 4 mm diameter), or 4 dram screw cap vials containing 90 percent EtOH for 1.5 min., using an ultrasonic cleaner, 2. Structures and eggs were then transferred from the 90 to 95 percent EtOH, sonicated for an additional 1.5 min., and then left to sit 10 min., 3. Structures and eggs were then transferred from 95 to 100 percent EtOH, sonicated again for 1.5 min., and left to sit for 10 min., 4a. The lateral stylets, subgenital plates and ova were then transferred into 100 percent acetone and sonicated for a final 1.5 min., then mounted, after having been air dried on forceps tips, to an aluminum stub using double-stick copper tape, 4b. The epiproct (a partially membranous structure that would shrink or wrinkle in 4a above), was then transferred through 2, 30 min. washes of hexamethyldisilazane (HMDS), then mounted after air dried on the tips of forceps to an aluminum stub, 5. Stubs were coated with 150–300 Å of gold using a Polaron Instruments “cool” sputter coater, Unit E5100 (Quorum Technologies Ltd. (QT), East Sussex, UK, http://www.quorumtech.com/) for 1.5–2.5 min., at a voltage of 20 mA.

All structures were studied using a JEOL® scanning electron microscope Model JSM-T300 (JEOL USA, Peabody, MA, http://www.jeol.com/). Lateral views of the epiproct and its modified setae, posterior view of lateral stylets, female subgenital plate, and views the ovum and its micropyles, chorionic structure, collar area, and whole ova, were photographed at several magnifications. The morphological descriptions of all life stages in the text herein are given in detail as lists in the Appendix.

Illustrations of nymph habitus, male head and pronotum, aedeagus, epiproct and internal basal anchor were made using hand-drawn tracings obtained from the ZEISS® drawing apparatus. Also, notes concerning setation, pigmentation and scale bar were

made. The tracings were scanned as black and white drawings and saved as 1200 dpi graphic (.tif) files. These computer files were opened in a graphic drawing/illustration program as independent layers to be used as a template to create entirely new digital illustrations using precise drawing tools to retrace every line made in the original tracings, and to stipple pattern and add setae and spinules.

Scanning electron micrographs made of nymphal mouthparts previously by B.P. Stark (Stewart and Stark 1988, 2002) were utilized for descriptions and are presented in Figs. 4–11. The geographic distribution (Fig. 2) represents only confirmed locations. The states within the distribution lists represent all published accounts, those with citations following were not confirmed during this project and further field collecting will be required.

Results

Taxonomic Characters

Internal male genitalia.—The terminology used to describe aedeagal characters is based on Szczytko and Stewart (1979) Alexander and Stewart (1999) and Stark and Nelson (2000). The aedeagus of *Isogenoides* species is fairly uniform in shape from base to apex, usually without a developed median body. The apex of the aedeagus consistently bears a pair of long, finger-like lobes laterally (Fig. 21, 22) and only one species possesses an additional, larger, ventral plate-like pair (Figs. 1A AED, 127). Spinulae are indistinct, sparse, minute, clear, erect hair-like setae not grouped into patterns. The setae are restricted to either partially or fully covering the pair of lateral finger-like lobes.

External male genitalia.—The epiproct is large, its apex usually partially sclerotized (Fig. 1A-C EPI), but may be mostly membranous (Fig. 147). The apical and lateral membranous portions are densely covered with minute scale-like spinulae (Figs. 1C EPI, 142), and the species are distinctive. The epiproct is attached to a sclerotized, internal basal anchor at a hinged-junction (Fig. 1C IBA). Lateral stylets (Fig. 1C LS) are attached by thin membrane at the base of the epiproct. Together, these structures are connected by the cowl (Fig. 1A COW) and are movable. The epiproct is capable of reaching above the dorsal surface of the tenth tergite (Fig. 1A), sometimes fully everted and thus reaching an anterior extension (Fig. 148). The degree to which this occurs depends on how much the folded, sock-like membranous cowl unfolds during extrusion. The hemitergal processes (Fig. 1B HTP) of the tenth tergum vary in density setae, length and shape. The tips of these processes may extend posteriorly (Fig. 1B), internally and anteriorly (Fig. 13), or internally and slightly posteriorly (Fig. 33).

Female genitalia.—The subgenital plate (Fig. 20) is typically extended over sternum 9 to various degrees. The posterior margin is highly variable.

Nymph.—The typical color of these moderately large nymphs is brown to dark brown, with only one species that is mostly yellow. The dorsum of the head possesses the typical perlodid M-pattern, although in one species it is usually mostly demarked by clothing setae. The pronotal discs are typically marked with a variable, lightly pigmented centralized pattern and both genders possess moderately long silky setae along the ecdysal suture. A new mandible character identified during this project tentatively divides the species into to equal sized groups. Under high magnification (50x or more) the left and usually right ventral basal margin of the distal-most

mandibular-cusp either possess an indistinct or distinct row of denticles (Figs 3–10), but is variable in three species.

Ovum.—All *Isogenoides* species are triangular in cross-section and have stalked collars with three stabilizing carinulae at each anterior angle (Fig. 100), except one species whose collar lacks the carinulae (Fig. 24). In all but one species, the stalk has even apical margins, only one is deeply incised between the stabilizing carinulae (Fig. 119). The chorion is relatively smooth (Fig. 44), or it may be modified with granular or globular processes (Fig. 82). Micropyle orifices occur sub-equatorially and in at least one species, may be partially covered by sperm guides (Fig. 139).

Pigment patterns.—Head, thorax and abdomen pigment patterns are reported in descriptions and used in the species key but caution must be exercised when using patterns because they are known to be variable within a species or population. Whenever possible, the details reported are differentiated between those of recently preserved specimens and those of older personal or museum materials.

Keys To The North American *Isogenoides*

(Each key couplet emphasizes diagnostic characters in descending order of importance. See synonymy of *I. krumholzi* with *I. doratus* in *I. doratus* species diagnosis, leaving 8 currently recognized species)

Adult Males

1. Apical sclerotized process present at tip of epiproct (Figs. 72, 110, 129) .....(2)
   Apical sclerotized process absent at tip of epiproct (Figs. 147, 159, 160) .....
   .....*I. zionensis*

2.(1). Apical process divided into two anteriorly directed, partially sclerotized hooks

(Fig. 112); posterior margin of epiproct with long, curved, lash-like tabular spine arising from just above mid-length as seen in lateral view (Fig. 110) …….. *I. olivaceus*

Apical process not divided anteriorly, completely sclerotized as a single hook or with grove (Figs. 36, 74, 131); posterior margin without long lash-like spine (Figs. 34, 72, 129) ……(3)

3.(2). Posterior margin of epiproct with paired, ventrally directed hooks or spines (can be difficult to see if epiproct not everted or extended, some dissection of the membranous cowl covering the lateral stylets may be required) (Figs. 34, 53, 129) ..…….(4)

Posterior margin of epiproct without paired, ventrally directed hooks or spines (Figs. 18, 72, 90) …….....(6)

4.(3). Apical process of epiproct modified, with deep internally sclerotized grove (Figs. 129, 141); paired, ventrally directed hooks on posterior margin heavily sclerotized, stout, their position from apex about 1/5 to 1/6 total epiproct length in lateral view …..…….. *I. varians*

Apical process of epiproct with single, stout, posteriorly, or posteriorly and ventrally directed hook (Figs. 34, 46, 129); paired, ventrally directed spines on posterior margin lightly sclerotized, slender, their position from apex 1/3 to 1/6 total epiproct length in lateral view ……..……..(5)

5.(4). Paired, ventrally directed posterior epiproct hooks slightly sclerotized and short (easily obscured by folding of epiproct tissue in cleared or older specimens), their position from apex about 1/3 to 1/2 total epiproct length in lateral view (Figs. 34, 45) ……..... *I. doratus*

Paired, ventrally directed posterior epiproct hooks moderately sclerotized and longer than above, their position from apex about 1/5 to 1/6 total epiproct length in lateral view (Figs. 53, 64, 65) ….……..... *I. elongatus*

6.(3). Head with large, yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly past epicranial suture intersection, ending inside interocellar area (Fig 95); epiproct apical hook long, its extension from epiproct about equal to epiproct width in lateral view (Figs. 90, 102, 103); from dorsal view, hemitergal lobes with only small, hardly visible membranous area connected to mesoanterior wing-like internal basal anchor sclerites (Fig. 89) ……..…….. *I. hansoni*

Head without yellow area extending from posterior margin into ocellar triangle, or, if interocellar area with median, longitudinal light area, then not yellow (Figs. 19, 77); epiproct apical hook short, its extension from epiproct less than epiproct width in lateral view (Figs. 18, 72); from dorsal view, hemitergal lobes connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Figs. 13, 14, 71) ……..…(7)

7.(6.) Apical 1/3 of lateral stylets in lateral view above widely expanded region, with margins sub-triangulate, gradually tapering to apex, forming bluntly pointed tips (Figs. 72, 86); generally, in non-everted specimens in dorsal view, inner-posterior angles of hemitergal lobes forming obtuse angles or evenly curved (Fig. 71); inner-rounded margins of distal-most anteriorly directed lobes in contact at most, anteriorly ……*I. frontalis*

Apical 1/3 to 1/2 of lateral stylets in lateral view above narrowly expanded region, with margins nearly parallel, forming narrowly rounded tips (Figs 18, 29); generally, in non-everted specimens in dorsal view, inner-posterior angles of hemitergal lobes forming nearly right angles or angulate (Fig. 14); inner-angulate margins of distal-most anteriorly directed lobes in contact nearly their entire lengths ……..... *I. colubrinus*

Adult Females

(Female diagnoses, except when distributions are allopatric or associated with their males, are problematic due to intraspecific subgenital plate variations and consequent character overlap for some species)

1. Head with large, yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly past epicranial suture intersection, ending inside interocellar area like male (Fig 95); subgenital plate posterior margin moderately rounded, usually less than 3/4 width of 8th sternum and produced from 1/2 to 3/4 length of 9th sternum (Figs. 96, 106) …..……..... *I. hansoni*

Head without yellow area extending from posterior margin into ocellar triangle, or, if interocellar area with median, longitudinal light area, then not yellow like males (Figs. 19, 58, 114, 152) …….....(2)

2.(1). Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum; produced from 1/4 to 3/4 length of 9th sternum, broadly rounded posterior margin with variable, deep, mesoposterior U or V-shaped notch (Figs. 20, 76) ……...(3)

Subgenital plate otherwise, when present, mesoposterior emargination smaller than above (Figs. 39, 115, 134) …….....(4)

3.(2). Of western distribution; from the Saskatchewan Rivers watersheds of south-central Saskatchewan southward and westward and possibly The Pas – Manitoba (Fig. 2) ……..……..……..... *I. colubrinus*

Of eastern distribution, from central and far eastern Saskatchewan and eastward and southward of Manitoba (Fig. 2) ..... *I. frontalis*

4.(2). Subgenital plate with broadly rounded posterior margin; mesoposterior margin variable (Fig. 39, 115, 134) …….(5)

Subgenital plate with quadrate or truncate posterior margin (57, 153) ……....(7)

5.(4). Subgenital plate produced from 1/3 to 2/3 length of 9th sternum (Figs. 39) .....(6)
Subgenital plate produced from 3/4 to entire length of 9th sternum (Fig. 134, 144); mesoposterior emargination variable, usually with slightly produced protrusion, sometimes emarginated, vestigial or absent; cerci, antennae, femur-tibia joints and wing veins all dark brown, almost black in recently preserved specimens ……..... *I. varians*

6.(5). Subgenital broad at base, its width approximately 3/4 width of 8th sternum (Figs. 39, 49); mesoposterior margin of plate variable, with small, slightly protruding nipple-like knob; small, slightly rounded emargination; small, emarginated, slightly protruding double nipple-like knob; or with margin entire; caution: characters and distributions may overlap in Michigan and Québec (Fig. 2) ……..……..... *I. doratus*
Subgenital plate moderately broad at base, its width usually less than 3/4 width of 8th sternum (Figs. 115, 125); mesoposterior margin of plate variable, with either a broad-shallow, or narrow-moderately deep emargination; caution: characters and distributions may overlap in Michigan and Québec (Fig. 2) ..……..... *I. olivaceus*

7.(4). Subgenital plate broad at base, its width from 2/3 to 3/4 width of 8th sternum; produced from 1/4 to 1/2 length of 9th sternum; posterior margin nearly quadrate or truncate with variable mesoposterior characters; usually with small, slightly protruding nipple-like knob (Figs. 57, 68); sometimes small, slightly rounded emargination; small, emarginated, slightly protruding double nipple-like knob; or margin entire or weakly and broadly emarginated its entire width; caution: characters and distributions may overlap in New Mexico, Colorado, Utah, and Arizona (Fig. 2) .. *I. elongatus*
Subgenital plate moderately broad at base, its width approximately 2/3 width of 8th sternum, a few sometimes wider; produced from 1/4 to 1/3 length of 9th sternum; posterior margin nearly quadrate or truncate with variable mesoposterior characters; usually with small to moderate, rounded, protruding nipple-like knob (Figs. 153, 163); sometimes small to moderate, emarginated, protruding double nipple-like knob; or nearly entire with vestigial emarginated double-protrusions barely visible; caution: characters and distributions may overlap in New Mexico, Colorado, Utah, and Arizona (Fig. 2) ..……..... *I. zionensis*

Mature Nymphs

(Pigment patterns are based on live or recently preserved specimens; may appear faded or variable in older specimens. *I. zionensis* – *I. elongatus* and *I. colubrinus* – *I.*

frontalis may be further tentatively separated by detailed comparison using written descriptions and distribution or when correlated with their males)

1. Denticles or serrations along inner margin of distal-most, ventral cusp of one or both mandibles usually small and inconspicuous (Figs. 3, 4, 6, 8) .....(2)
   Denticles or serrations along inner margin of distal-most, ventral cusp of one or both mandibles usually large, stout and conspicuous, large denticles usually present well beyond basal 1/2 of cusp (Figs. 5, 7, 9, 10) .....(5)

2.(1). Male with obvious developing lash-like epiproct; abdominal segments with a well defined anterior transverse dark band and a thin posterior band (Fig. 107). .....*I. olivaceus*
   Male with developing epiproct variable, not protruding and lash-like (Figs. 11, 31, 69); abdominal terga, with only an anterior transverse dark band (Figs. 11, 31, 69) .....(3)

3. (2). M-pattern of head not completely enclosed anteriorly by dark pigment, only two thin, curved, dark bars prominent (Fig. 31); dorsum of nymph with densely scattered dark, long, appressed clothing setae, visible at low magnification (clothing setae fade to clear or golden in older material) ..... *I. doratus*
   M-pattern of head usually completely enclosed by dark pigment (Figs. 11, 69); clothing setae, when present, short, clear, not contrasting in color with erect, stout setae .....(4)

4. (3). Anterior transverse dark pigment bands of most abdominal segments covering 1/2 or less of terga (Fig. 11); of western distribution; from the Saskatchewan Rivers watershed of south-central Saskatchewan southward and westward and possibly The Pas – Manitoba (Fig. 2) ..... *I. colubrinus*
   Anterior transverse dark pigment bands of most abdominal segments covering 1/2 or more of terga (Fig. 69); of eastern distribution, from central and far eastern Saskatchewan and eastward and southward of Manitoba (Fig. 2) ..... *I. frontalis*

5. (1). Abdominal terga with distinct, dark, anterior and posterior transverse bands on segments 1–9 (Fig. 88); preserved material with anterior bands sometimes thin, partially to completely hidden by overlapping segment's margin; segment 10 usually with only anterior margin dark, with variable lateral dark banding ..... *I. hansoni*
   Abdominal terga having only one narrow, transverse, dark pigment band at anterior margin (Fig. 126); or anterior and posterior dark bands narrow and usually interrupted mesally (Fig. 145); or wide, dark anterior bands usually covering most of terga (Fig. 50) .....(6)

6. (5). Head pattern indistinct, without defined light M-pattern (Fig. 126); abdominal

terga with narrow, dark, anterior, transverse band; dorsum of almost entire nymph, especially pronotum with sparse to lightly scattered long, dark, clothing setae, lighter colored toward head and posterior abdominal segments on older specimens ..... *I. varians*

Head pattern distinct, with defined M-pattern at least posteriorly (Figs. 50, 145); abdominal terga with either wide, dark, anterior, transverse bands covering most of surface (Fig. 50); or anterior and posterior dark bands narrow and usually interrupted mesally (Fig. 145) .....(7)

7. (6) Dark to light brown pigment over most of dorsum; M-pattern can be enclosed anteriorly with continuous dark band; pigment patterns fade quickly in alcohol (Fig. 50) ..... *I. elongatus*

Moderate to light brown pigment over most of dorsum; M-pattern usually not enclosed anteriorly with continuous dark band; pigment patterns fade quickly in alcohol (Fig. 145) ..... *I. zionensis*

Ova

(Based on limited SEMs)

1. Collar without three stabilizing carinulae at each anterior angle (Fig. 24) ..... *I. colubrinus*

Collar with three stabilizing carinulae at each anterior angle (Fig. 43, 100) .....(2)

2. (1). Chorion mostly smooth (Figs. 44, 139) .....(3)

Chorion granular (Figs. 63, 82, 101, 120, 158) .....(4)

3. (2). Micropyle orifices with cup-like sperm guides (Fig. 139) ..... *I. varians*

Micropyle orifices without sperm guides (Fig. 44) ..... *I. doratus*

4. (2). Micropyle orifices at ends of micropylar tubes (Figs. 82 120, 158) .....(5)

Micropyle orifices on top of micropylar knobs (Figs. 63, 101) .....(7)

5. (4). Collar deeply incised between carinulae at anterior angles (Fig. 119) *.I. olivaceus*

Collar not deeply incised between carinulae (Figs. 82, 157) .....(6)

6. (5). Micropyle orifices located within unevenly raised, slightly carinate, apical portions of micropylar tubes (Fig. 158) ..... *I. zionensis*

Micropyle orifices located within evenly raised, smoothly rounded, apical portions of micropylar tubes (Fig. 82) ..... *I. frontalis*

7. (4). Chorion surface with sparse, prominent, granular processes (Fig. 63) ..... *I. elongatus*

Chorion surface with dense, low, granular processes (Fig. 101) ..... *I. hansoni*

Genus *Isogenoides* Klapálek

Isogenus (*Isogenoides*) Klapálek, 1912: 4(1):57. Type Species: *Perla* (*Isogenus*) *frontalis* (Newmann 1838) = *Isogenoides frontalis* (Newman).
Isogenus, Needham and Claassen, 1925, 2:68.
Isogenus (*Isogenoides*) Claassen, 1940, 232:105.
Isogenoides Hanson, 1943, 29:658.
Isogenus (*Isogenoides*) Ricker, 1952, 18:105.
Isogenoides Illies, 1966, 82:363.
Isogenoides Zwick, 1973, 94:231.

Nearctic Species

Adult – Body length: medium to large (13–20 mm). Wings: macropterous to brachypterous (3.1–19 mm), usually hyaline, sometimes partially fumose; veins brown to black. Gills: remnant pair present at the basal-lateral margins of submentum, length about 2 times width. Head: brown to black, generally with yellow, roughly triangular region below juncture of lateral arms and stem of occipital sutures, these extending anteriorly and laterally to various degrees. Two variable, usually flattened, diffuse to dark brown markings, each located between anterior-most portion of M-pattern and anterior margin of head, rarely absent or connected to anterior margin. Two variable-, elongate-, or irregular-shaped dark markings, each located along inner margins of antennal bases. Two conspicuous, irregular- to bean-shaped, medium to dark brown, raised rugosities positioned anterolaterally of lateral ocelli, rarely with irregular-shaped dark markings below. Occiput and usually post-ocular area with small, irregular-shaped, raised and un-raised slightly darker rugosities, sometimes faded, blending with background. Interocellar area with small, semicircular, dark brown, almost black, markings along inner margins of lateral ocelli and posterior margin of anterior ocellus, sometimes absorbed by large, wide, dark, longitudinal bands, or lateral ocellar dark

markings extend anteriorly and laterally, connecting to posterior margin of large, irregular-shaped rugosities; outer margins of lateral ocelli either similar to surrounding background, unpigmented, or darker than surrounding background pigment. Transverse M-pattern raised, usually dark brown at least along median arms. Irregularly-shaped, lateral, light areas usually present above the bases of antennae or palpi. Clothing setae of head fine, clear, with tiny semicircular yellow spots marking attachment points on dark pigment. Antennae usually with partially erect fine setae or rarely with a mixture of partially erect and erect setae along apical margins. Labrum with short, stout, erect brown setae along anterior margin, sclerotized at base connecting to frons. Pronotum: light brown to brown with median light stripe; approximately square to trapezoidal, anterior margin broadly rounded, lateral margins nearly straight, sometimes irregular, true lateral margins folded under ventrally but sometimes visible dorsally, posterior margin variable, with narrow to broadly rounded mesoposterior emargination, rarely rounded. Rugosities dark, raised, without setae, rounded, irregular-shaped, generally concentrated along lateral margins of median light stripe and below anterior transverse furrow, few laterally. Transverse grooves or furrows along the anterior and posterior margins variously pigmented. Mesosternum: Y arms of mesosternum meeting posterior corners of furcal pits, a distinctive median longitudinal suture connects the fork of the Y with the anterior transverse ridge. Body color: variable, brown to dark brown, occasionally almost black with lighter, variable pattern. Abdominal terga usually brown to dark brown with paired median and lateral muscle-scars usually light. Terga 1–3 and last segment either similar to adjacent segments, lighter brown to yellow, unpigmented or with other various light pigmentation;

cerci light brown to almost black. Male terminalia-tenth tergum: tenth tergum completely cleft with variable-sized membranous area anteriorly, bearing sclerotized hemitergal lobes posteriorly; these usually clothed with variable amounts of short–long, thin, golden hair-like setae with 10–42 variously shaped, stout spinulae or sensilla basiconica. 10th tergite in dorsal view begins anteriorly with median membranous area flanked laterally by two narrow, roughly pointed, anterior sclerotized margins expanding laterally and posteriorly into hemitergal lobes. Cowl (membranous, folded, sock-like tissue) located between and under hemitergal lobes, attached around base of epiproct, internal basal anchor and lateral stylets. Dorsal wing-like sclerites of internal basal anchor triangular, fragile, located immediately posterior of cleft 10^{th} tergal margins. Dissected internal basal anchor in lateral view, stout, flattened at juncture with ventral epiproct; hollowed dorsally, rod-like extension continues anteriorly and dorsally meeting variable-shaped laterally expanded plates, partially sclerotized anterior keel-like sclerite broadly rounded. Epiproct and lateral stylets present medially and posteriorly, enclosed by cowl posteriorly unless genitalia are everted. Paragenital plates of tenth segment variously shaped, attached to cowl flanking epiproct and stylets laterally. Subanal lobes large, attached to cerci basally, enclose epiproct posteriorly in non-everted males. Sternal Lobe: lobe-like mesoposterior abdominal margin of sternum seven usually rounded but not extending past posterolateral margins. Sometimes no apparent rounding of posterior margin detectable, or the rounded appearance is due to pigmentation rather than the posterior margin. Epiproct: either membranous or sclerotized at apex, forming a curved posteroventrally directed hook or deep groove. Variable anterior and posterior support sclerites present, membranous areas near distal margin armed with modified

scale-like setae. Aedeagus: entirely membranous with one pair of distinct posterolateral lobes, usually bearing scattered minute clear spinulae.

Female – Subgenital plate: generally extended from posterior margin of eighth sternum over ninth, variable shapes including slightly quadrate, broadly to slightly rounded with or without mesoposterior emargination or protrusion. Some species are known to be highly variable in this character.

Nymphs – Body length: medium to large (10–20 mm). Body color: variable, yellow, olive, and brown to dark brown. Intersegmental membranes cream with variable patches of minute light brown freckle-like circular markings. Dorsum of head with arms of epicranial suture defined by thin light line extending anteriorly along outer margins of lateral ocelli; 4–8 long, erect, clear setae scattered on frons. Ocelli large, appear to have black semicircular markings below anterior and along inner margins of lateral ocelli. Occiput with large, approximately oval light areas usually partially filled with faint, light tan reticulated pattern that fades over time. Gills: present only at the basal-lateral margins of submentum, length about two times their width. Maxilla: lacinia triangular, bidentate, with distinct knob posterior to subapical tooth, inner margin with more or less complete row of setae, maxillary palpus 5-segmented. Labrum: mesoanterior margin usually with small hump, anterior margin with long thin setae, dorsal surface with or without smaller clothing setae. Mandible: Left and right mandibles with 6 teeth arranged in distal and proximal groups of 3 cusps each; under high magnification, ventral basal margin of distal-most cusp variable, from indistinct row of small, vestigial denticles to distinct row of large, sharp denticles reaching about 1/2 length of inner margin; basal margin of proximal group with dense tuft of long thin setae (acanthae) continuing

ventrally to about 1/2 length of inner margin; long ventral patch of long, fine setae extending from base of distal-most cusp to base of mandible; dorsal surface with short patch of long, fine setae extending from below basal-most proximal cusp to base of acanthae. Labium: labial palpus 3-segmented, paraglossae larger than and forward of glossae. Pronotum: variable, usually with lighter brown to yellow or unpigmented central areas, sometimes forming a narrow-broken to wide-continuous longitudinal stripe, margins fringed almost entirely with variable-length peg-like setae, sometimes with mesoanterior or posterior margin long silk-like setae. Dorsum covered with variable clothing setae and variable, short or minute erect golden spines sparsely interspersed. Median longitudinal rows of moderately spaced, long, silky setae positioned along dorsal suture. Mesosternum: Y-arms of mesosternum meeting posterior corner of furcal pits and a distinctive median longitudinal suture connect the fork of the Y with the anterior transverse ridge. Legs cream, occasionally with longitudinal brown band on ventrolateral outer femur surface becoming diffuse proximally, or with indistinct light brown or tan band along dorsal margin and diffuse distal area on ventrolateral outer surface of femur; stout spinulae scattered on outside femur surface, heavily concentrated in dorsal narrow band, sparsely scattered in ventral thick band; long, fine, silky setae in dense dorsal row between inner and outer bands of stout spinulae. Abdominal terga: variable, light to dark brown, olive or yellow, and with or without variable dark anterior or anterior and posterior pigment bands. Stout intercalary spinules numerous laterally, interrupted by median rows of long, silky setae. Posterior setal row of female 8th sternum interrupted and notched mesoposteriorly. Cerci with complete dorsal fringe of long silky setae.

Ova – General shape oval, triangular cross section. Color yellow to light brown. Collar: with variable apically flanged rim, usually stalked with slightly elevated and irregular carinae, and usually with three large stabilizing carinulae broadly connecting collar to each anterior angle. Chorion: smooth with globular processes to granular. Micropyles: variable in number, usually subequatorial. Sperm guides presumable fragile when present, known to brake off near micropylar orifice during preparation in two species.

Diagnosis and Discussion – *Isogenoides* is morphologically most similar to *Hydroperla* Frison, and they share the following characters: 1. Male 10th tergum completely divided; 2. Male epiproct present and variable; 3. Male lateral stylets usually present; 4. Male sternum 7 modified, either slightly produced or variable pigmentation along posterior margin; 5. Adult and nymph submental gills long, at least 2 times as long as wide; 6. Irregular network of supplementary crossveins absent in apical area of wings; 7. Egg cross section triangular; 8. Nymph lacinia triangular, subapical lacinial tooth placed forward. *Hydroperla* differs from *Isogenoides* in that males of one species lack lateral stylets, the armature of the epiproct differs in variable degrees, and the nymph left mandible has only four cusps.

Isogenoides is widely distributed, transcontinental in the North, with eastern species found from Atlantic Canada and Minnesota, to Mississippi and South Carolina, and western species throughout the western cordillera and Pacific Northwest, from Alaska to Saskatchewan and south from northern California to New Mexico. The species are usually found in small mountain rivers supporting trout populations, but can inhabit even smaller creeks feeding these rivers or at the headwaters of rivers, and

some species also have the ability to inhabit large silty rivers with less stable substrates. In western creeks, rivers it can either be the lone large perlodid or often share the habitat with *Diura knowltoni* (Frison) or *Skwala americana* (Klapálek). Emergence is earlier for eastern species, beginning around March-April and western species beginning around May-June, both continuing about a month.

Species Descriptions

Isogenoides colubrinus (Hagen) (Figs. 3, 11–30)

Isogenus colubrinus Hagen, 1874. Holotype ♀, Snake River, ID (Museum of Comparative Zoology)
Perla titusi Banks, 1918. Syn. design. Needham and Claassen, 1925
Isogenus colubrinus, Needham and Claassen, 1925
Isogenus colubrinus, Claassen, 1940 (in part)
Isogenoides frontalis, Hanson, 1943
Isogenus (Isogenoides) frontalis colubrinus, Ricker, 1952
Isogenoides colubrinus, Illies, 1966

Additional references: *Isogenus colubrinus*, Claassen 1930 (Nymph illustrated from unknown location). *Isogenus (Isogenoides) frontalis colubrinus*, Jewett, 1959 (male and female genitalia); Jewett, 1960 (male and female genitalia). *Isogenus colubrinus*, Ricker, 1964 (distribution map). *Isogenoides colubrinus*, Gaufin et al., 1966, (keys, illustrations, distribution, and biology for Utah species); Baumann et al., 1977, (keys, illustrations, and distribution for Rocky Mountain species).

Male. — Macropterous to partially brachypterous. Length of forewings 9.5–15 mm; length of body 15–20 mm. General body color brown to dark brown. Dorsum of head with thin light area along mesoanterior margin (Fig. 19); anterolateral large, irregular-shaped, light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, nearly triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures; tiny dark brown setae absent. M-pattern raised, without setae, dark brown pigmentation

beginning at anterior ocellus, fading to light brown and yellow at anterior-most portions, these blending with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margin of antennal bases (Fig. 19). Interocellar area variable, usually brown, similar to surrounding area, sometimes darker brown pigment enters area laterally, connecting lateral ocelli to anterior ocellus, forming two, wide, slightly angled, longitudinal bands extending anteriorly from lateral ocellus to inner, posterior margins of M-pattern (Fig. 19). Antennae medium to dark brown, with 50+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown pigment; background pigmentation light brown or brown, anterior and posterior margins dark brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above furrow (Fig. 19). Mesonotum dark brown with variable areas of light pigment centrally and along sutures of notal plates. Legs light brown to yellow with transverse, dark brown band covering above and below femur-tibia joints; outside, lateral femur with densely scattered clear, short, thin clothing setae; dark brown, tiny, erect setae broadly scattered, nearly same length as clothing setae; without 1–2 hairless streaks; tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins. Abdomen brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by

preceding segment's posterior margin; first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to yellow; dorsum entirely covered with dense, short, clear clothing setae becoming longer on posterior expanded segments; dorsolateral humps on terga 6–9 expanded into paired pin cushion-like swellings, those on 7th segment largest, sometimes extending beyond anterior margin of segment eight, covered with long, clear to golden, thin clothing or hair-like setae (Fig. 12–14). Sternal lobe large, located along mesoposterior margin, broadly rounded, with lighter, almost yellow pigment, surrounding areas dark brown, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view of everted specimens with lobe apices directed medially and anteriorly, inner-posterior margins usually sharp, sometimes obtuse, but slightly angled (Fig. 13); non-everted specimens with distal-most, anteriorly directed lobes generally in contact along entire inner-median margins, inner-posterior margins usually angulate (Figs. 12, 14); connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Figs. 12, 14); 20–34 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 12–14); short, dark, scattered, erect setae and long, clear, moderately dense, fine setae concentrated along posterior and inner margins. Epiproct apex in lateral view with single, stout, light brown or golden, posterior and ventrally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 18, 26, 27); posterior margin without pair of ventrally directed sclerotized hooks; in lateral view, under high magnification, anterior portion of epiproct with long, apically straight, narrow, moderately pointed, scale-like setae, lateral margins with deep apically angled serrations (Fig. 28); anterior support sclerite trifid in

anterior view, lateral and median arms longer than base (Fig. 16), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 18, 26), median arm narrow, tapered to sharp pointed apex ending before reaching 1/2 length of entire epiproct (Fig. 16); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins subequal above hole to nearly 3/4 length of total epiproct, tapering to narrow distal portion, joining inner, posterior margin of apical hook (Fig. 15). Internal basal anchor in anterior view with wide base tapering gradually to nearly parallel where anterior keel-like sclerite connects, expanding laterally into short, rounded plates (Fig. 17); large, wing-like triangular sclerites dorsal-most, directed posterolaterally, central notch absent. Lateral stylets in lateral view with long, narrow base (Fig. 18); expanded areas variable, at approximately 1/2 to 2/3 total length from base; apical portion narrow at expanded region, margins mostly parallel, narrowly rounded tips; in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 15, 29); apical portions smoothly curved, apices directed slightly laterally. Paragenital plates large, situated laterally on membranous tissue (cowl) surrounding epiproct, partially hidden dorsally by hemitergal lobe and posteriorly by subanal lobes in non-everted specimens. Subanal lobes rounded with dorsally and posteriorly directed lobe completely sclerotized outside, membranous inside, sclerotized plate light brown without membranous notch; long, fine hair-like setae located centrally and along posterior margins of sclerotized plate. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 21, 22); tiny, clear, erect setae sparsely scattered mostly along posterior margin of lateral lobe; two smaller lobes dorsally, close to distal

margin, may not be fully everted, their inverted bases only visible (Fig. 21); one wide broadly rounded lobe projects slightly from distal margin. Cercal segments brown, 25–26 segments, basal-most not fully sclerotized; basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter on distal segments; tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal segments; groups of 3–10 long, golden, stout setae project ventrally from mesoposterior margin; distal segments covered with short, dense, clear clothing setae.

Female. — Macropterous. Length of forewings 15–18 mm; length of body 14–19 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum, produced from 1/4 to 3/4 length of 9th sternum, broadly rounded posterior margin with deep, variable, mesoposterior notch, from U to V-shaped (Figs. 20, 30); dark pigment mostly anterior and lateral with two smaller dark markings on plate, below mesally-angled posterior margins of abdomen, some females have a slightly darkened posterior margin including mesoposterior emargination.

Nymph. — General body color light brown to yellow with light and dark markings (Fig. 11). Antennae light brown almost golden; with short, erect, golden peg-like setae arranged as whorls around apical margins, sometimes a few on dorsal surface of first segment; usually with short sparse row of long, fine, clear, silky setae beginning on segment two, ending on segment 7–8; short, clear, intersegmental clothing setae sparsely scattered on segment one; minute, erect setae scattered on segment two. Dorsum of head with contrasting pigment pattern; fine, short, clear, clothing setae

sparsely scattered; light colored narrow band forming M-pattern between antennal bases and median ocellus; anterior transverse brown band thick, completely enclosing M-pattern anteriorly; anterior margin with narrow transverse light band, brown area below, enclosing M-pattern with two small transversely flattened, thin, light areas above anterior-most portions of M-pattern; two large, sometimes boot-shaped dark markings on anterolateral margins between antennal bases and labrum; labrum with two semicircular dark markings along anterior margin; variable, flatly rounded, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern; small, triangular-shaped light areas along outer lateral margins of lateral ocelli; recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows. Interocular area brown, similar to adjacent areas; post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction. Lacinia with 1 axilary seta, 18–21 marginal setae below subapical tooth, 12–16 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp variable, usually short indistinct row of small, vestigial denticles, occasionally distinct row of large, sharp denticles reaching about 1/2 length of inner margin (Fig. 3). Submental gills at least 2x as long as width at base. Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs; anterior transverse furrow thick, dark brown, almost black anteriorly, anterior margin light brown to brown; posterior transverse furrow thin, medium to dark brown, almost black posteriorly; posterior margin

light brown to brown, light lateral margins; central pronotum distinctly patterned with two, nearly parallel brown bands on each side of light colored dorsal suture, extending posteriorly almost entire length of discs; light colored, variable-shaped, curved, light stripes radiate from anteromesal to posterolateral areas, remainder mostly brown; anterior and posterior margins with row of stout peg-like setae, sometimes with 1–4 longer setae near corners, lateral margin setae usually smaller, sometimes interrupted or absent near mid-length; posterior margin peg-like setae with long, stout, erect setae scattered, long, fine, silky setae usually near dorsal suture; pronotum covered with moderately sparse, short, clear, clothing setae. Meso-Metanota light brown, usually a large pair of mesoanterior light oval areas on each disc, sometimes single, tear-drop shaped, with thin longitudinal dark band bisecting oval areas faded or absent in preserved specimens; long, thin, curved, posteriorly widened, light areas mesally, near dorsal suture, between mesoanterior light areas; variable heart-shaped light area along posterior half of dorsal suture. Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–9, segment one all brown except small, rounded, light area at mesoposterior margin, 10th tergum either with band as above or expanded posteriorly, following the contour of posterior margin, then cutting sharp anteriorly at lateral margins; short, clear, clothing setae interspersed between stout spines; posterior margins with continuous row of spinules, those on 10th tergum usually a single, approximately linear row. Posterior setal row of male 8th abdominal sternum sometimes interrupted mesally in mature and immature nymphs. Cercal segments golden brown; apical whorl of short, stout setae, those located at mesoposterior apical margin becoming longer on distal segments.

Ovum. — General shape oval, triangular cross section (Fig. 23). Color light brown. Length 229–249 µm, width 147 µm. Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, without three large stabilizing carinulae at each anterior angle (Fig. 24). Chorionic surface granular (Fig. 24). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located on low slightly carinate, micropylar knobs (Fig. 25).

Material examined. — TYPES: *I. colubrinus*, Holotype ♀, IDAHO: Snake River, C. Thomas, Pin# 263 (MCZ); *Perla titusi*, Holotype ♀, IDAHO: Blackfoot, 1918, 1 ♀, (Type 10046) (NMNH). Paratypes, *I. hudsonicus*; ALASKA: Fort Yukon, 1877, 1 ♀, (Slide# 1794.1) (CUIC).

Additional specimens — *CAN*: ALBERTA: Location ?, Lesser Slave Lake, 21/VI/1929, C.P. Alexander, 1 ♂ (NMNH), Edmonton, River ?, 7/VI/1925, O. Bryant, 1 ♂ (CUIC), Fort McKay, Athabasca R., 17/VI/1977, N. Hynes, 1 Nymph (NMNH), Fort McMurray, River ?, 14/VII/1976, D. Barton, 1 ♀ (NMNH), Jasper Park, Athabasca Falls, 19/VIII/1952, M.E. Smith, 1 ♀ (NMNH), Jasper, Atherhaskae L., 28/VII/1946, M.E. Smith, 1 ♀ (NMNH).

BRITISH COLUMBIA: Location ?, Big Thompson R., 13/VI/1924, Collector ?, 1 ♂ (INHS), Location ?, Trout R., 20/VI/1958, C.H. Lindroth, 2 ♂ (NMNH), Lillooet, River ?, 4/VI/1958, C.H. Lindroth, 1 ♂ (NMNH), Spences Bridge, River ?, 25/VI/1956, R. Coleman, 1 ♂ (NMNH), Spences Bridge, River ?, 25/VI/1956, R. Coleman, 2 ♀ (NMNH).

YUKON: Alaskan Hwy. (mile 117) N.W. of Burwash Landing, Kluane R., 28/VI/1996, J. C. Abbott & K. W. Stewart, 2 ♂, 3 ♀, 4 exuviae (UNT), Alaskan Hwy N. of Whitehorse, Takhini R., 27/VI/1996, J.C. Abbott & K.W. Stewart, 1 ♀ (UNT).

USA: ALASKA: 8 mi. W. of Yukon Border, USGS map Coleen (B-1), Porcupine R., 1/VII/1982, J. Boron, 1 ♂, 1 ♀ (UNT), Near Fairbanks, Tannanah R., K.W. Stewart & ? Cartner, 10 exuviae (UNT), At confluence with Charley R., Yukon R., 8/VII/1974, D. Huggins, 1 ♂ Nymph cleared, 1 exuvia (UNT), At Circle, Banks of Yukon, 12/VII/1952, D.L. Carlson, 1 ♀ (NMNH), Near Ft. Yukon, River ?, Date ?, T.E. Winekoff, 1 ♂ (NMNH).

ARIZONA: Navajo Co., West Fort Apache, White R., 3/VI/1982, R.W. Baumann & ? Clark, 1 ♂, 4 ♀ (BYU).

CALIFORNIA: Tehama Co., Near Red Bluff, Sacramento R., 31/III/1965, S.G. Jewett, Jr., 12 ♂ (BYU), Near Red Bluff, Sacramento R., 12/IV/1960, Collector ?, 1 ♂, 7 exuviae (BYU).

COLORADO: Moffat Co., Echo Park Dinosaur Nat. Mon., Yampa R., 3/V/1987, C. MacVean, 1 ♀ (CSU), 1 mi. N. of Maybell in spider web, Yampa R., 4/VIII/1973, B.P. Stark & R.W. Baumann, 3♂, 1 ♀ (BS), At Maybell, Yampa R., 29/VI/1968, B.R. Oblad, 2 ♂, 4 ♀ (BYU), BLM Pub. Lands at Twelvemile Gulch & Cross Mtn Canyon, Yampa River, 13/III/2000, J.B. Sandberg, 25 Nymphs (JBS), BLM Pub. Lands at Twelvemile Gulch & Cross Mtn Canyon, Yampa River, 21/V/2000, J.B. Sandberg, 8 ♂, 9 ♀ (reared), 30 Nymphs (JBS).

IDAHO: County ?, Rarie ?, South Fork Snake R., 23/VI/1949, T. Purcell, 1 ♂, 1 ♀ [10 *I. elongatus* males in vial] (NMNH), County ?, Rarie ?, South Fork Snake R.,

23/VI/1949, T. Purcell, 1 ♀ [three *I. elongatus* females in vial] (NMNH), Idaho Co., 8 mi. S. of White Bird, Salmon R., 2/IV/1977, D. Funk, 4 Nymphs (UNT), Latah Co., Moscow, River ?, Date ?, J.M. Aldrich, 2 ♂, 2 ♀ (NMNH).

MONTANA: County ?, Forsythe, Yellowstone R., 5/V/1973, ?. Roemhild, 2 ♀, 3 exuviae (UNT), County ?, At Sawmill Gulch Station, Clark Fork R., 9/III/1957, ? Williamson & ? Spindler, 11 Nymphs (UNT); Custer Co., At Miles City, Yellowstone R., 5/V/1973, ? Roemhild, 3 ♂, 4 ♀ (UNT), At Miles City, Yellowstone R., 22/III/1973, ? Roemhild, 3 nymphs (UNT); Dawson Co., At Intake, Yellowstone R., 16/V/1975, R.L. Newell, 1 ♀ [one *I. elongatus* male in vial] (UNT); Park Co., At mouth of Shields R. NE of Livingston, Yellowstone R., 15/IV/1973, ? Roemhild, 1 nymph (UNT).

OREGON: Benton Co., Corvallis, River ?, 6/IV/1932, V. Star, 1 ♀ (NMNH), Corvallis, River ?, April, Collector ?, 1 ♂ (NMNH), Corvallis, River ?, 21/III/1932, Collector ?, 1 ♀ (NMNH); Clackamas Co., Oregon City, River ?, 18/IV/1948, S.G. Jewett, 1 ♂ (NMNH); Curry Co., Wedderburn, River ?, 19/IV/1952, W.M. Morton, 2 ♂ (NMNH); Umatilla Co., Location?, River?, 24/VI/1882, S. Henshaw, 1 ♂ (CUIC); Wasco Co., The Dalles, River ?, 23/VI/1882, S. Henshaw, 1 ♂ (NMNH).

UTAH: Summit Co., Smith & Morehouse Camp Gr., Smith & Morehouse Cr., 04/V/1992, R.W. Baumann & ? Zenger, ♂♂, ♀♀ (BYU); Unitah Co., Green R. Camp Gr. Dinosaur Nat. Mon., Green R., 20/V/1994, G. Skiba, 1 ♂ (CSU), Split Mt. Camp Gr. Dinosaur Nat. Mon., Green R., 23/V/1974, B. P. Stark & D. Alstead, 1 ♂ epiproct, 7 Nymphs, 1 exuvia (BP), Split Mt. Camp Gr. Dinosaur Nat. Mon., Green R., 23/V/1974, B. P. Stark & D. Alstead, 3 Nymphs (BYU).

WASHINGTON: Chelan Co., Orondo, Columbia R., 10/VI/1914, E.J. Newcomer, 1 ♂ (NMNH), Pateros, Columbia R., 27/V/1929, M.D. Leonard, 2 ♂ (NMNH), Pateros, Columbia R., 27/V/1929, M.D. Leonard, 1 ♀ (NMNH), Pateros, Columbia R., 27/V/1929, M.D. Leonard, 2 ♂, 2 ♀ (NMNH).

WYOMING: Sweetwater Co., Near Granger, Green R., 24/VI/1948, D.G. Denning, 1 ♀ (NMNH); Teton Co., Near Hoback Junction, Snake R., 16/VI/1973, J. Perry, 1 ♂ (BYU).

Distribution. — CANADA: Alberta, British Columbia, Manitoba (Ricker 1952), Northwest Territories, Saskatchewan (Dosdall and Lemkuhl 1979), Yukon Territory; USA: Alaska, Arizona, California, Colorado, Idaho, Montana (Gaufin et al. 1972), Oregon, Utah, Washington, Wyoming (Fig. 2).

Diagnosis and Discussion. — Males of *I. colubrinus* are most similar to *I. frontalis* and females cannot be separated except by geographic proximity. Males can be distinguished by their longer, parallel margined, lateral stylet apices (Figs. 18, 29). The inner-posterior sclerotized corner of hemitergal lobes ranged from nearly right to obtuse angles, especially in everted males (Figs. 12, 13); non-everted males with distal-most, anteriorly directed lobes generally in contact along entire inner-median margins, inner posterior margins usually angulate (Fig. 14). Recently preserved nymphs can tentatively be separated by the thickness of anterior abdominal banding (Fig. 11). Ova are distinctive in that only they lack three large stabilizing carinulae at the juncture of the collar and the 3-anterior edges.

This species has a broad transcontinental distribution in the West from Alaska to Saskatchewan (Dosdall & Lemkuhl 1979) and possibly “The Pas” in Manitoba (Ricker

1964) where overlap may occur with *I. frontalis*. Its distribution continues southward into northern California, Montana to northern Colorado and southern-most into northern Arizona (Fig. 2). No life history or biological studies have been done on this species. Sympatric distributions with *I. elongatus* may occur in the Yampa, Columbia and South Fork Snake Rivers. These must be considered tentative due to the age of the museum holdings and recent collecting trips have not been conducted.

Adults reared in the laboratory and from known field collections indicate that emergence begins in March to June and continues until mid-August, with peak emergence occurring in late May-June.

Isogenoides doratus (Frison), comb. nov. (Figs. 4, 31–49)

Hydroperla dorata Frison, 1942. Holotype ♂, Pere Marquette R., Near Baldwin, MI, (Illinois Natural History Survey), (Figures of ♂ and ♀ are *I. hansoni*)
Isogenus (Isogenoides) doratus, Ricker, 1952, (Figures of ♂ epiproct do not match the Holotype male, no written descriptions provided)
Isogenus (Isogenoides) krumholzi, Ricker, 1952, Holotype ♂: Pine River, Walkers Bridge, Lake County, MI (Illinois Natural History Survey), **NEW SYNONYMY**
Isogenoides doratus, Hanson, 1953, (First description and figures of ♂ paratype).
Isogenoides doratus, Illies, 1966

Additional references: *I. krumholzi* and *I. doratus*, Hitchcock 1974 (keys to adults, larvae, descriptions, and illustrations), Surdick and Kim 1975 (*I. doratus* collection records are now *I. hansoni* Holotypes), Kondratieff 2004 (Figures of ♂ epiproct without posterior pair of small ventrally directed spines).

Male. — Macropterous. Length of forewings 13–14.5 mm; length of body 13–17 mm. General body color brown to dark brown. Dorsum of head with rounded, light area offset from mesoanterior margin by thin brown band along anterior margin (Fig. 38); anterolateral large, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial

sutures; tiny dark brown setae absent. M-pattern raised, without setae, dark brown throughout most of pattern, beginning to fade to light brown and yellow just past anterior-most portions, these blending in pigmentation with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 38). Interocellar area brown with dark brown pigment entering laterally, dark brown areas connecting lateral ocelli to anterior ocellus, extending towards eyes, ending below large, lateral, medium brown rugosities; medium brown areas above dark brown areas; dark and medium brown areas form two, wide, slightly angled, longitudinal bands extending mesoanteriorly from lateral ocelli to inner, posterior margins of M-pattern (Fig. 38). Antennae dark brown, with 46+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, with almost black pigment along posterior borders; background pigmentation light brown, anterior and posterior margins dark brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 38). Mesonotum dark brown with variable and irregular areas of light pigment centrally and along dorsal suture, appearing as continuation of pronotal median longitudinal stripe. Legs light brown to dark brown with transverse, dark brown band covering above and below femur-tibia joints, outside, lateral femur with densely scattered, clear, short, thin clothing setae; without dark brown, thin, erect setae; 1–2

variable length, thin hairless streaks on outside surface, tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins. Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin; first two terga with variable-shaped unpigmented areas, hemitergal and subanal lobes light brown to dark brown; dorsum entirely covered with dense, short, clear clothing setae not becoming longer on posterior, slightly expanded segments, except longer on hemitergal lobes; dorsolateral humps on terga 6–9 small, hardly evident in dorsal view, posterolateral margins of 7th tergum slightly swollen laterally, not posteriorly, posterolateral swollen area of tergum 8 with narrow transverse patches of slightly longer, golden, hair-like setae (Fig. 32, 33). Sternal lobe large, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with lighter brown or yellow pigment, the lightest along posterior margin, then blending anteriorly into surrounding darker pigment, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view with lobe apices directed medially and posteriorly, apical margins broadly rounded, connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 33); 16–20 golden, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 32, 33); short, dark, erect setae scattered posteriorly on lobe apex continuing laterally and anteriorly, these interspersed within long, numerous, golden, hair-like setae concentrated along posterior margin of lobe apex. Epiproct apex in lateral view with single, stout, posteriorly directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 34, 45, 46);

posterior margin with slightly sclerotized pair of short, ventrally directed hooks, their position from apex about 1/3 to 1/2 total epiproct length in lateral view; in lateral view, under high magnification, anterior portion of epiproct with long, apically curved, moderately narrow, sharply tipped, scale-like setae, lateral margins with deep apically angled serrations (Fig. 47); anterior support sclerite trifid in anterior view, lateral arms as long as or slightly longer than base (Fig. 37), median arm approximately 1/2 as long as base, lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 34, 45), median arm wide at base, tapered gradually to sharp pointed apex ending before reaching 1/2 length of entire epiproct (Fig. 37); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins tapering slightly, then expanding slightly, to join laterally at about 1/2 to 2/3 total epiproct length from base to pair of short, lightly sclerotized, ventrally directed hooks, support sclerite continuing dorsally, tapering again gradually to broad apical point, ending near base of apical hook (Fig. 36). Internal basal anchor in anterior view hour glass-shaped with wide base tapering gradually to where anterior keel-like sclerite connects, expanding laterally into long, rounded lateral plates (Fig. 35); small, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located, wide, rounded notch. Lateral stylets in lateral view with long, narrow base (Fig. 34); expanded areas at nearly 2/3 total length from base, parts of expanded region lightly sclerotized, barely visible along inner and dorsal margins; apical 1/3 narrow at expanded region, margins tapering gradually to narrowly rounded tips, angled margins minutely serrate; in anterior or posterior view, stylet appearing slightly wider than in lateral view (Figs. 36, 48); apical portions smoothly

curved, apices directed dorsally. Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens. Subanal lobes rounded with posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate with long U-shaped membranous notch reaching approximately 1/3 length from apex in posterior view; long, fine hair-like setae on dorsal yellow portion, short, clothing setae on basal brown portion of sclerotized plate. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 40, 41); tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes; two smaller pairs of lobes dorsally and ventrally, close to distal margin (Figs. 40, 41). Cercal segments brown, 21–25 segments, basal-most not fully sclerotized; basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter on distal segments; tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal segments; groups of 3–6 long, golden, stout setae project posteroventrally from mesoposterior apical margin; distal segments covered with short, dense, clear clothing setae.

Female. — Macropterous. Length of forewings 15.5–17 mm; length of body 15–19 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum, produced from 1/3 to 2/3 length of 9th sternum; broadly rounded posterior margin with variable mesoposterior characters (Figs. 39, 49): mesoposterior margin of subgenital plate with small, slightly protruding nipple-like knob, mesoposterior margin of subgenital plate with small, slightly rounded emargination, mesoposterior margin of subgenital

plate with a small, emarginated, slightly protruding double nipple-like knob, and posterior margin of subgenital plate entire; dark pigmentation mostly anterior and lateral with two, smaller dark brown markings on plate, below mesally-angled posterior margins of abdomen, these markings enclosed by larger light brown markings.

Nymph. — General body color light brown to yellow with light and dark markings (Fig. 31). Antennae light tan almost yellow; with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segments 1–3; usually with long sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 17–18; short, clear, intersegmental setae apparently absent. Dorsum of head with contrasting pigment pattern; fine, long, dark clothing setae densely scattered; light colored narrow band forming M-pattern between antennal bases and median ocellus open mesoanteriorly; anterior transverse brown band reduced to two short, thin, anteriorly curved bands beginning along anterolateral margins, incompletely enclosing M-pattern anteriorly; anterior margin usually with broad transverse light band, generally extending mesoposteriorly to median ocellus, sometimes this area with faded light brown pigment, brown bands below partially enclosing M-pattern without two light areas; two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum; labrum with two semicircular dark markings along anterior margin; variable, flatly rounded, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern diffuse, open posteriorly and laterally; large, irregular-shaped light areas along outer margins and above lateral ocelli, continuing laterally, almost to bases of antennae, recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending

posteriorly from below epicranial arm sutures to inner occipital spinule rows. Interocular area brown, sometimes with variable, mesoposterior light brown marking extending posteriorly from below anterior ocellus to epicranial intersection; post ocular and occipital spinule rows thin with many peg-like spinulae, longer, stout, spine absent in occipital row near post ocular row junction; occipital spinule row sometimes interrupted by small gap. Lacinia with 1 axilary seta, 18–20 marginal setae below subapical tooth, 10–13 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp with short, indistinct row of small denticles reaching about 1/2 length of cusp (Fig. 4). Submental gills approximately 2x as long as width at base. Pronotum mostly light brown dorsally and laterally with variably patterned central area light brown, tan or yellow; anterior transverse furrow thick, dark brown, almost black, anterior margin brown; posterior transverse furrow thin, dark brown, almost black, tapering to narrow mesal points; posterior margin brown, light lateral margins; central area of pronotum distinctly patterned with two oppositely curved, narrow, light brown bands on each side of dorsal suture, extending posteriorly, almost entire length of discs, these mesal longitudinal bands fade to light tan or yellow in older specimens; a second, variable-shaped light brown band positioned between mesal longitudinal band and about 1/2 width of disc, rarely remains intact after 1-year in alcohol; irregular, variable-shaped network of light brown bands laterally, these variously joined to lateral, posterior borders of anterior furrows, sometimes beginning below posterior border markings, connecting posteriorly to irregular-shaped, light brown markings above posterior furrow; anterolateral, lateral, and posterior margins with continuous, similarly sized, stout, peg-

like setae; pronotum covered with moderately dense, long, dark, clothing setae. Meso-Metanota light brown, usually with three pairs of mesoanterior, light, oval areas distinct; in older specimens, thin brown bands enclosing these areas fade, leaving golden spinulae and dark clothing setae to indicate their original margins; another longer light area positioned below the three light oval areas extends anterolaterally, meeting anterior, thick, dark brown transverse band; wide heart-shaped light area along posterior half of dorsal suture open posteriorly, or partially closed with variable pigment in some; wide, brown band or bands begin abruptly in mesolateral area of wing pad, continue on mesal posterior angles, reaching the posterior angled margin of wing pad. Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–10, segment one usually all brown except small, rounded, light area at mesoposterior margin, 10th tergum usually similar to 9th; long, dark, clothing setae interspersed between stout spines; posterior margins with continuous row of spinules, those on 10th tergum usually a single, approximately linear row. Posterior setal row of male 8th abdominal sternum usually interrupted mesally in mature nymphs. Cercal segments yellow; apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.

Ovum. — General shape oval, triangular cross section (Fig. 40). Color light brown. Length 385 µm, width 243 µm. Collar with slight apically flanged rim, stalked with slightly elevated and irregular carinae, and with 3 large stabilizing carinulae broadly connecting collar to each anterior angle (Fig. 41). Chorionic surface smooth, with only very small, scattered globular structures (Fig. 42). Hexagonal follicle cell impressions

absent. Micropyle row subequatorial; orifices located on low, smooth, rounded micropylar knobs (Fig. 42).

Material examined. — TYPES: *I. doratus*, Holotype ♂ (reared) and allotype ♀ (reared), MICHIGAN: Lake Co., Near Baldwin, Pere Marquette R., 10/V/1940, T. Frison & H. Ross, Vial #'s 1546 & 1547 (INHS); *I. krumholzi* Holotype ♂, MICHIGAN, Lake Co., Walker's bridge, Pine R., Collector ?, Vial# 1554, (INHS). Paratypes; *I. doratus*, MICHIGAN: Lake Co., Near Baldwin, Pere Marquette R., 10/V/1940, T. Frison & H. Ross, 1 ♂ (reared) # 2519, (INHS).

Additional specimens — *CAN*: QUEBEC: Cage face camp, R. Nabisipi, 18/VI/1962, G. Shooner, 6 ♂, 8 ♀ (UM), Cage et Cuisine du camp, R. Nabisipi, 15/VI/1962, G. Shooner, 4 ♂, 6 ♀ (UM).

USA: IOWA: Boone Co., Fraser, Des Moines River, 25/IV/1947, W.Starrett, 2 ♂, 3 ♀ (BYU), Fraser, Des Moines River, 25/IV/1947, W.Starrett, 1 ♂, 5 ♀ (BYU); Lyon Co., Lakewood Corner, Rock River, 09/II/2002, J. Sandberg, 8 ♂ (reared), 6 ♀ (reared), 6 Nymphs (JBS); Sioux Co., Hwy. 18, N. of Rock Valley, 10/IV/1996, B.C. Kondratieff & R.W. Baumann, 3 ♂, 5 ♀, 1 Nymph, 10 exuviae (CSU), Hwy. 18, N. of Rock Valley, 10/IV/1996, B.C. Kondratieff & R.W. Baumann, 9 ♂, 13 ♀, 4 Nymphs, 22 exuviae (CSU), Hwy. 18, N. of Rock Valley, 10/IV/1996, R.W. Baumann & B.C. Kondratieff, 2 ♂, 2 ♀ (BYU); Story Co., 2 mi. N. of Ames, S. Skunk R., 10/IV/1952, R. Whitney & J. Forney, 1 ♂, 1 ♀, 1 Nymph (UNT), 2 mi. N. of Ames, S. Skunk R., 10/IV/1952, R. Whitney & J. Forney, 4 ♂, 4 ♀ (BYU).

MICHIGAN: Lake Co., Near Baldwin, Pere Marquette R., 9-10/V/1940, T. Frison & H. Ross, 1 Nymph (INHS), Near Baldwin, Pere Marquette R., 9-10/V/1940, T. Frison

& H. Ross, 10 exuvia (INHS), Near Baldwin, Pere Marquette R., 9-10/V/1940, T. Frison & H. Ross, 2 exuvia (INHS), Walker's bridge, Pine R., 10/IV/1999, B. Kondratieff & J. Sandberg, 1 ♂ (reared), 1 ♀ (reared) (JBS).

Distribution. — CANADA: Manitoba (Stark et al. 1986), Québec; USA: Iowa, Michigan, Minnesota (Ricker 1952 under *I. krumholzi*) (Fig. 2).

Diagnosis and Discussion. — Males of I. doratus are most similar to *I. elongatus* and females can only be tentatively separated from *I. olivaceus* by their slightly broader subgenital plate (Figs. 39, 115). Males can be distinguished by the presence of paired, small, ventrally directed, lightly sclerotized hooks positioned at approximately mid-length of posterior margin of epiproct (Fig. 34). *Isogenoides doratus* differs most from *I. elongatus* in several details including the size and placement of paired, posterior and ventrally directed hooks more ventral along posterior margin of epiproct (Fig. 34, 53), and the presence of long, stout spinulae near anterior margins of hemitergal lobes (33, 52).

No data on life history or general biology are available. Based on the material examined and laboratory rearing, emergence occurs from late-April to mid-June. This species inhabits medium sized rivers.

I propose here, that *I. doratus* (senior synonym) and *I. krumholzi* (junior synonym) are the same, after critical examination of both Holotype males and the above additional specimens. The reasoning for this synonymy is as follows: 1. Ricker's description of *I. krumholzi* (1952) was basically correct, the illustration and written description although brief, fit the specimen held in (INHS) Plecoptera # 1554. 2. The first true written description and illustration set for *I. doratus* (Paratype male, INHS #

1547, and Holotype male, INHS # 1546) by Hanson (1953), finally became available 10-years after the original description (Frison 1942). 3. The above types both fit the primary and secondary descriptions and illustrations for *I. krumholzi* (Ricker 1952) and *I. doratus* (Hanson 1953). 4. Because Frison's *I. dorata* was the first published account of the name (although incorrectly described and illustrated), it has date and time priority (ICZN) over *I. krumholzi*.

Isogenoides elongatus (Hagen) (Figs. 3, 11–30)

Isogenus elongatus Hagen, 1874. Holotype ♀, Foothills of Colorado and Ogden, UT, (Museum of Comparative Zoology)
Isogenus (Isogenoides) Klapálek, 1912
Isogenus elongatus, Needham and Claassen, 1925
Isogenus elongatus, Claassen, 1940
Isogenoides elongatus, Hanson, 1943
Isogenus (Isogenoides) elongatus, Ricker, 1952
Isogenoides elongatus, Illies, 1966

Additional references: *Isogenoides zionensis*, = *I. elongatus* in Gaufin et al. 1966 (adult key); Baumann et al. 1997 (adult, nymph key).

Male. — Macropterous to partially brachypterous. Length of forewings 9.5–15 mm; length of body 15–20 mm. General body color brown to dark brown. Dorsum of head with thin light area along mesoanterior margin (Fig. 19); anterolateral large, irregular-shaped, light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, nearly triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures; tiny dark brown setae absent. M-pattern raised, without setae, dark brown pigmentation beginning at anterior ocellus, fading to light brown and yellow at anterior-most portions, these blending with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margin of antennal bases (Fig.

19). Interocellar area variable, usually brown, similar to surrounding area, sometimes darker brown pigment enters area laterally, connecting lateral ocelli to anterior ocellus, forming two, wide, slightly angled, longitudinal bands extending anteriorly from lateral ocellus to inner, posterior margins of M-pattern (Fig. 19). Antennae medium to dark brown, with 50+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown pigment; background pigmentation light brown or brown, anterior and posterior margins dark brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above furrow (Fig. 19). Mesonotum dark brown with variable areas of light pigment centrally and along sutures of notal plates. Legs light brown to yellow with transverse, dark brown band covering above and below femur-tibia joints; outside, lateral femur with densely scattered clear, short, thin clothing setae; dark brown, tiny, erect setae broadly scattered, nearly same length as clothing setae; without 1–2 hairless streaks; tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins. Abdomen brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin; first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to yellow; dorsum entirely covered with dense, short, clear clothing setae becoming longer on posterior expanded

segments; dorsolateral humps on terga 6–9 expanded into paired pin cushion-like swellings, those on 7th segment largest, sometimes extending beyond anterior margin of segment eight, covered with long, clear to golden, thin clothing or hair-like setae (Fig. 12–14). Sternal lobe large, located along mesoposterior margin, broadly rounded, with lighter, almost yellow pigment, surrounding areas dark brown, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view of everted specimens with lobe apices directed medially and anteriorly, inner-posterior margins usually sharp, sometimes obtuse, but slightly angled (Fig. 13); non-everted specimens with distal-most, anteriorly directed lobes generally in contact along entire inner-median margins, inner-posterior margins usually angulate (Figs. 12, 14); connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Figs. 12, 14); 20–34 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 12–14); short, dark, scattered, erect setae and long, clear, moderately dense, fine setae concentrated along posterior and inner margins. Epiproct apex in lateral view with single, stout, light brown or golden, posterior and ventrally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 18, 26, 27); posterior margin without pair of ventrally directed sclerotized hooks; in lateral view, under high magnification, anterior portion of epiproct with long, apically straight, narrow, moderately pointed, scale-like setae, lateral margins with deep apically angled serrations (Fig. 28); anterior support sclerite trifid in anterior view, lateral and median arms longer than base (Fig. 16), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 18, 26), median arm narrow, tapered to sharp pointed apex ending before reaching 1/2 length of

entire epiproct (Fig. 16); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins subequal above hole to nearly 3/4 length of total epiproct, tapering to narrow distal portion, joining inner, posterior margin of apical hook (Fig. 15). Internal basal anchor in anterior view with wide base tapering gradually to nearly parallel where anterior keel-like sclerite connects, expanding laterally into short, rounded plates (Fig. 17); large, wing-like triangular sclerites dorsal-most, directed posterolaterally, central notch absent. Lateral stylets in lateral view with long, narrow base (Fig. 18); expanded areas variable, at approximately 1/2 to 2/3 total length from base; apical portion narrow at expanded region, margins mostly parallel, narrowly rounded tips; in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 15, 29); apical portions smoothly curved, apices directed slightly laterally. Paragenital plates large, situated laterally on membranous tissue (cowl) surrounding epiproct, partially hidden dorsally by hemitergal lobe and posteriorly by subanal lobes in non-everted specimens. Subanal lobes rounded with dorsally and posteriorly directed lobe completely sclerotized outside, membranous inside, sclerotized plate light brown without membranous notch; long, fine hair-like setae located centrally and along posterior margins of sclerotized plate. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 21, 22); tiny, clear, erect setae sparsely scattered mostly along posterior margin of lateral lobe; two smaller lobes dorsally, close to distal margin, may not be fully everted, their inverted bases only visible (Fig. 21); one wide broadly rounded lobe projects slightly from distal margin. Cercal segments brown, 25–26 segments, basal-most not fully sclerotized; basal 5–10 segments completely covered

with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter on distal segments; tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on apical segments; groups of 3–10 long, golden, stout setae project ventrally from mesoposterior margin; distal segments covered with short, dense, clear clothing setae.

Female. — Macropterous. Length of forewings 15–18 mm; length of body 14–19 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum, produced from 1/4 to 3/4 length of 9th sternum, broadly rounded posterior margin with deep, variable, mesoposterior notch, from U to V-shaped (Figs. 20, 30); dark pigment mostly anterior and lateral with two smaller dark markings on plate, below mesally-angled posterior margins of abdomen, some females have a slightly darkened posterior margin including mesoposterior emargination.

Nymph. — General body color light brown to yellow with light and dark markings (Fig. 11). Antennae light brown almost golden; with short, erect, golden peg-like setae arranged as whorls around apical margins, sometimes a few on dorsal surface of first segment; usually with short sparse row of long, fine, clear, silky setae beginning on segment two, ending on segment 7–8; short, clear, intersegmental clothing setae sparsely scattered on segment one; minute, erect setae scattered on segment two. Dorsum of head with contrasting pigment pattern; fine, short, clear, clothing setae sparsely scattered; light colored narrow band forming M-pattern between antennal bases and median ocellus; anterior transverse brown band thick, completely enclosing M-pattern anteriorly; anterior margin with narrow transverse light band, brown area

below, enclosing M-pattern with two small transversely flattened, thin, light areas above anterior-most portions of M-pattern; two large, sometimes boot-shaped dark markings on anterolateral margins between antennal bases and labrum; labrum with two semicircular dark markings along anterior margin; variable, flatly rounded, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern; small, triangular-shaped light areas along outer lateral margins of lateral ocelli; recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows. Interocular area brown, similar to adjacent areas; post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction. Lacinia with 1 axilary seta, 18–21 marginal setae below subapical tooth, 12–16 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp variable, usually short indistinct row of small, vestigial denticles, occasionally distinct row of large, sharp denticles reaching about 1/2 length of inner margin (Fig. 3). Submental gills at least 2x as long as width at base. Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs; anterior transverse furrow thick, dark brown, almost black anteriorly, anterior margin light brown to brown; posterior transverse furrow thin, medium to dark brown, almost black posteriorly; posterior margin light brown to brown, light lateral margins; central pronotum distinctly patterned with two, nearly parallel brown bands on each side of light colored dorsal suture, extending posteriorly almost entire length of discs; light colored, variable-shaped, curved, light

stripes radiate from anteromesal to posterolateral areas, remainder mostly brown; anterior and posterior margins with row of stout peg-like setae, sometimes with 1–4 longer setae near corners, lateral margin setae usually smaller, sometimes interrupted or absent near mid-length; posterior margin peg-like setae with long, stout, erect setae scattered, long, fine, silky setae usually near dorsal suture; pronotum covered with moderately sparse, short, clear, clothing setae. Meso-Metanota light brown, usually a large pair of mesoanterior light oval areas on each disc, sometimes single, tear-drop shaped, with thin longitudinal dark band bisecting oval areas faded or absent in preserved specimens; long, thin, curved, posteriorly widened, light areas mesally, near dorsal suture, between mesoanterior light areas; variable heart-shaped light area along posterior half of dorsal suture. Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–9, segment one all brown except small, rounded, light area at mesoposterior margin, 10th tergum either with band as above or expanded posteriorly, following the contour of posterior margin, then cutting sharp anteriorly at lateral margins; short, clear, clothing setae interspersed between stout spines; posterior margins with continuous row of spinules, those on 10th tergum usually a single, approximately linear row. Posterior setal row of male 8th abdominal sternum sometimes interrupted mesally in mature and immature nymphs. Cercal segments golden brown; apical whorl of short, stout setae, those located at mesoposterior apical margin becoming longer on distal segments;

Ovum. — General shape oval, triangular cross section (Fig. 23). Color light brown. Length 229–249 µm, width 147 µm. Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, without three large stabilizing

carinulae at each anterior angle (Fig. 24). Chorionic surface granular (Fig. 24). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located on low slightly carinate, micropylar knobs (Fig. 25).

Material examined. — TYPES: *I. elongatus*, Holotype ♀, IDAHO: Ft. Hill, learfenter?, '73, [Handwritten labels illegible], pin# 263, (MCZ).

Additional specimens — COLORADO: County ?, Location ?, Poudre R., June 1889, Collector, 1 ♂ (CUIC); County ?, Platte Canyon, River ?, Date ?, Dyar & Caudell, 1 ♂ [Parallotype?] (NMNH); Eagle Co., Location ?, Eagle R., 31/III/1997, C.D.O.W., 16 Nymphs (CSU); Freemont Co., Cotopaxi 6400', 13/VI/1949, C. Alexander, 2 ♀ (NMNH); Garfield Co., Rt. 13, Rifle, Colorado R., 7/IV/1989, B.C. Kondratieff, 2 Nymphs (CSU), At Rifle, Colorado R., 21/II/1994, B.C. Kondratieff,, 9 ♂, 3 ♀, 1 Nymph, 9 exuviae (CSU), Hwy 13, Rifle park, Colorado R., 30/V/1999, J. Sandberg, 20 exuviae (JBS), Hwy 13, Rifle park, Colorado R., 12/III/2000, J. Sandberg, 12 ♂ (reared), 5 ♀ (reared), 29 Nymphs, (JBS); Grand Co., Rt. 40 bridge, Colorado R., 18/VI/1986, B.C. Kondratieff, 1 ♀ (CSU), At Hot Sulfur Springs, Colorado R., 1/V/1981, K.W. Stewart, B.P. Stark, D. Zeigler, & W.D.S., 13 Nymphs (UNT), At Granby, Hwy 40 bridge, 01/VI/1999, J. Sandberg, 10 ♂, 20 ♀, 21 Exuviae (JBS); Rio Blanco Co., Meeker, White R., 21/VI/1953, A Barnum, 1 ♂ (BYU); Routt Co., 10 mi. E. of Craig, Yampa R., 20/VI/1968, B. Oblad, 1 ♂, 1 ♀ (BYU), 1 mi. E. of Hayden, Yampa R., 20/VI/1968, B. Oblad, 1 ♂, 1 ♀ (BYU).

IDAHO: County ?, Rarie?, S.F. Snake R., 23/VI/1949, T. Purcell, 4 ♂, 1 ♀ (NMNH); County ?, Rarie?, S.F. Snake R., 23/VI/1949, T. Purcell, 10 ♂ [1 male, 1 female *I. colubrinus* in vial] (NMNH); County ?, Rarie?, S.F. Snake R., 23/VI/1949, T.

Purcell, 3 ♀, [1 female *I. colubrinus* in vial] (NMNH); Lemhi Co., Wagon hammer spring Hwy. 93 S. of North Fork, North Fork Salmon R., 17/VI/1965 A.R. Gaufin, 1 ♂ (BYU).

MONTANA: Broadwater Co., At Logan, Gallatin R., 2/V/1972, ? Roemhild, 1 ♂ (UNT), At Townsend bridge, Missouri R., 4/V/1936, H. Mills, 1 ♂ (INHS), At Townsend bridge, Missouri R., 4/V/1936, H. Mills, 2 ♂ (INHS), At Townsend, Missouri R., 04/V/1936, H. Mills, 3 ♂, 2 ♀ (BYU); Dawson Co., At Intake, Yellowstone R., 16/V/1975, R. Newell, 1 ♂ (UNT); Flathead Co., Walton ranger station at Essex, 3/VII/1970, R. Haick, 1 ♂ (NMNH); Park Co., Location ?, Yellowstone R., 5/IV/1974, R. Newell, 2 Nymphs (UNT), 5 mi. S. of Livingston, Yellowstone R., 15/IV/1973, ? Roemhild, 11 Nymphs (UNT), Rt. 89, Emigrant, Yellowstone R., 10/VI/1987, B.C. Kondratieff, 9 ♂, 3 ♀ (CSU), Sta. b, Yellowstone R., 5/IV/1974, R. Newell, 6 Nymphs (BYU); Gallatin Co., At Logan, Gallatin R., 13/IV/1985, D. Gustafson, 7 Nymphs (UNT); Missoula Co., Missoula, Bitterroot R., 11/V/1973, R. Haick, 2 ♀ (NMNH), Missoula, Clark Fork, ?/V/1949, ? Kohls, 2 ♂, 10 ♀ (NMNH), Missoula, At Rattlesnake Creek, Clark Fork, 5/V/1973, R. Haick & D. McAuliffe, 8 ♂, 10 ♀ (NMNH), Missoula, Clark Fork, 13/V/1973, R. Haick & D. McAuliffe, 3 ♂, 8 ♀ (NMNH), Missoula, Clark Fork, 3/V/1973, R. Haick, 1 ♀ (NMNH), Missoula, Clark Fork, 28/III/1973, R. Haick, 10 Nymphs, (NMNH), Craighead Apt. 116A, Clarks Fork Missouri R., 16/V/1969, M. Oblad, 1 ♀ (BYU); Ravalli Co., Woodside, Bitterroot R., 18/V/1955, D. Merkley, 1 ♂, 1 ♀ (BYU).

NEW MEXICO: Colfax Co., At Vernejo Park, Vernejo R., 23/IV/1986, B.C. Kondratieff, 1 ♂, 10 Nymphs (CSU); Lincoln Co., Near Ruidoso, Rio Ruidoso, 21/V/1972, S. Fiance, 1 Nymph (NMNH); San Miguel Co., At Pecos, Pecos R., 24/V/1974, M. & E. Cather, 1 ♂, 1 ♀ (BYU).

SOUTH DAKOTA: Pennington Co., Pactola inlet above Pactola Res., Rapid Cr., 6/VI/1995, R.W. Baumann & ? Huntsman, 9 ♂, 3 ♀ (BYU).

UTAH: Summit Co., Location ?, Weber R., 27/V/1962, A.W. Knight, 1 ♂, 1 ♀ (BYU); Location ?, Weber R., 1/VI/1962, A.W. Knight, 1 ♂, (BYU).

WASHINGTON: Chelan Co., Pateros, Columbia R., 27/V/1929, M. Leonard, 1 ♀ (NMNH).

WYOMING: Freemont Co., Rt. 287, S. of Dubois, Wind R., 7/VI/1987, B.C. Kondratieff, 6 ♂, 2 ♀, eggs, (CSU); Teton Co., W. of Jackson, Wind R., 25/VI/1995, B.C. Kondratieff, 1 ♂ (CSU), Rt. 22, 4 mi. W. of Jackson, Snake R., 8/VI/1987, B.C. Kondratieff & R.F. Kirchner, 7 ♂, 10 ♀, 6 exuviae, (CSU), Grand Tetons, Beaver Dick Lake, 10/VII/1941, W. Harrison, 1 ♀ (NMNH), At Moose, GTNP, 6650', Snake R., 28/VI/1964, J. Richardson, 1 ♂ (BYU), Near Hoback Junction, Snake R., 16/VI/1973, J. Perry, 1 ♂ (BYU).

Distribution. — CANADA: Alberta (Stark et al. 1986), British Columbia (Baumann et al. 1977), Manitoba (Stark et al. 1986); USA: Arizona (Baumann et al. 1977), Colorado, Idaho, Montana, New Mexico, South Dakota, Utah, Washington, Wyoming (Fig. 2).

Diagnosis and Discussion. — Males of *I. elongatus* are most similar to *I. doratus*. Males can be distinguished by their longer and more dorsally placed pair of ventrally directed hooks along the posterior margin of the epiproct (Fig. 53). Females can tentatively be separated from *I. zionensis* by their slightly broader subgenital plate (Figs. 57, 153). Nymph pigmentation, unless recently preserved or live, is variable but generally similar to *I. zionensis*. Nymphal species identification can be difficult when

distribution overlaps with *I. zionensis* or in areas of sympatry with *I. colubrinus*. A new character separating nymphs into two groups is the presence of large, distinct or small, indistinct ventral serrations on the distal-most mandibular cusp. This character is subjective and variable, especially in *I. elongatus* because mature specimens occasionally lack the diagnostically large serrations on one or both mandibles (Fig. 5). Therefore the key to nymphs for these species remains tentative until better characters are found. For now, when separating *I. colubrinus* nymphs from *I. elongatus*, the males of the later will have reduced wing pads (Fig. 50), this character however will not separate *I. elongatus* from *I. zionensis* nymphs.

This species is distributed throughout the west, mainly in cordilleran states. It exhibits a large amount of morphological variation in the shape of female subgenital plate and nymph pigmentation patterns of dorsal head and thorax. Variations in these characters were observed in single populations at several locations. Unfortunately, females of closely related species also vary greatly.

No data on life history or general biology are available. Based on the material examined and limited laboratory rearing, emergence occurs from late April to early July.

Isogenoides frontalis (Newman) (Figs. 6, 69–87)

Perla (Isogenus) frontalis Newman, 1838. Holotype ♀, Trenton Falls, NY, (British Natural History Museum)
Isogenus frontalis, Needham and Claassen, 1925 (in part)
Isogenus frontalis, Claassen, 1940 (in part)
Isogenus frontalis, Frison, 1942 (in part)
Isogenoides hudsonicus Hanson, 1943. Syn. Ricker, 1944
Isogenus (Isogenoides) frontalis, Ricker, 1952
Isogenoides frontalis, Illies, 1966

Additional references: *Isogenoides frontalis*, Ricker et al. 1968 (distribution), Hilsenhoff & Billmyer 1973 (keys, photographs of lacinia, distribution, and biology of Wisconsin species), Harper and Pilon 1975 (distribution), Shapas and Hilsenhoff

1976 (nymph feeding habits), Harper et al. 1991 (life cycle), Harper and Ricker 1994 (distribution), Kondratieff 2004 (distribution, description, figures and key to adults).

Male. — Macropterous. Length of forewings 15–17 mm; length of body 17–19 mm. General body color brown to dark brown. Dorsum of head with thin light area along mesoanterior margin (Fig. 77); anterolateral small, irregular-shaped, light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, nearly triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures; tiny, dark brown, erect setae sparsely scattered in basal occiput regions. M-pattern raised, without setae, dark brown pigmentation beginning at anterior ocellus, fading to light brown and yellow at anterior-most portions, these blending in pigmentation with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margin of antennal bases (Fig. 77). Interocellar area variable, usually brown with dark brown pigment entering laterally, sometimes completely darker than background, dark brown areas when present, connect lateral ocelli to anterior ocellus, extending towards eye, ending below large, lateral, medium brown rugosities; dark brown areas form two, wide, laterally directed bands, extending anterolaterally from lateral ocelli, reaching at least lateral wrinkled areas (fig. 77). Antennae medium to dark brown, with 52+/- segments, covered with dense, clear, partially erect, clothing setae and sparsely scattered, short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, anterior furrow filled with slightly darker brown pigment, posterior furrow filled with dark brown with almost black, thin ridges posteriorly; background pigmentation, anterior, and posterior margins brown; clothing setae short, densely

scattered with small yellow spots at attachment points, a few dark, short, erect, setae sparsely scattered posteriorly, some with tiny semicircular dark spots marking attachment points, these generally forming moderately spaced row near anterior margin. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe bowling pin-shaped (Fig. 77). Mesonotum dark brown with variable areas of light pigment centrally and along sutures of notal plates. Legs light brown to yellow with weak, transverse, brown band covering above and below femur-tibia joints, dark brown pigment usually forming variable dorsal, longitudinal stripes on femur; outside, lateral femur with densely scattered clear, short, thin clothing setae; dark brown, tiny, erect setae broadly scattered, nearly same length as clothing setae; with 1–2 variable length, thin hairless streaks on outer surface; tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins. Abdomen brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin; first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to yellow; dorsum entirely covered with dense, short, clear clothing setae becoming longer on posterior expanded segments; dorsolateral humps on terga 6–9 expanded into paired pin cushion-like swellings, those on 7th segment largest, sometimes extending beyond anterior margin of segment eight, covered with long, clear to golden, thin clothing or hair-like setae (Fig. 70, 71). Sternal lobe large, located along mesoposterior margin, broadly rounded, with lighter, almost yellow pigment, surrounding areas dark brown, posterior margin not extending past posterolateral

margins of 7th sternite. Hemitergal lobes in dorsal view of everted specimens with lobe apices directed medially and anteriorly, inner-posterior margins usually broadly rounded, appearing obtuse (Fig. 71); non-everted specimens with distal-most, anteriorly directed lobes generally in contact mesoanteriorly at most, inner-posterior margins usually evenly curved; connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 70, 71); 26–42 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 70, 71); short, dark, scattered, erect setae and long, clear, moderately dense, fine setae concentrated along posterior and inner margins. Epiproct apex in lateral view with single, stout, dark brown, posterior and ventrally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 72, 83, 84); posterior margin without pair of ventrally directed sclerotized hooks; in lateral view, under high magnification, anterior portion of epiproct with long, apically expanded, round tipped, scale-like setae, lateral margins without serrations (Fig. 85); anterior support sclerite trifid in anterior view, lateral arms longer than base (Fig. 75), median arm subequal, lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 72, 83, 84), median arm narrow, tapered to sharp pointed apex ending approximately at 1/2 length of entire epiproct (Fig. 75); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins tapering gradually from base to approximately 1/2 length of total epiproct, margins subequal to nearly 3/4 total length from base, tapering gradually to narrow distal portion, joining inner, posterior margin of apical hook (Fig. 74). Internal basal anchor in anterior view wide base tapering inwards at lower 1/4 length,

gradual outwards taper to approximately dorsal 1/2 length where anterior keel-like sclerite connects, gradually expanding into small, pointed lateral plates (Fig. 73); large, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located, narrow, elongated plate. Lateral stylets in lateral view with long, narrow base (Fig. 72); expanded areas variable, at nearly 2/3 total length from base, apical 1/3 wide, irregular-shaped at expanded region, margins sub-triangulate, tapering to bluntly pointed tips; in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 74, 75); apical portions irregularly-curved, apices angulate, directed laterally; Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens. Subanal lobes rounded with dorsally and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate light to dark brown with membranous notch broadly rounded along distal margin; long, fine hair-like setae scattered moderately over entire sclerotized plate, sometimes shorter setae on ventral portions. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral, apical margins (Figs. 78, 79); tiny, clear, erect setae sparsely scattered over entire lateral lobe margins; two smaller lobes dorsally, close to distal margin, may not be fully everted, their inverted bases only visible (Fig. 78); ventral wide, broadly rounded lobe projects slightly from distal margin. Cercal segments brown, 24–27 segments, basal-most not fully sclerotized; basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter distal segments; tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal

segments; groups of 3–10 long, golden, stout setae project ventrally from mesoposterior margin; distal segments covered with short, dense, clear clothing setae.

Female. — Macropterous. Length of forewings 17–19 mm; length of body 17–19 mm. General body color, and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum, produced from 1/4 to 3/4 length of 9th sternum, broadly rounded posterior margin with variable, deep, mesoposterior notch, from U to V-shaped (Figs. 76, 87); dark pigment patterns variable, from almost entirely brown to almost entirely yellow, consistently with two smaller dark markings on plate, below mesally-angled posterior margins of abdomen.

Nymph. — General body color brown with light and dark markings (Fig. 69). Antennae light brown; with short, erect, golden peg-like setae arranged as whorls around apical margins, sometimes a few on dorsal surface of first segment; usually with short sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 9–10; short, clear, intersegmental clothing setae scattered on segment one; minute, erect setae scattered on segment two. Dorsum of head with or without contrasting pigment pattern, sometimes mostly brown to dark brown; fine, short, clear, clothing setae usually sparsely scattered to absent; when present, light colored narrow band forming M-pattern between antennal bases and median ocellus, sometimes all brown; anterior transverse brown band thick, completely enclosing M-pattern anteriorly; anterior margin with narrow transverse light band, brown area below, enclosing M-pattern with two small transversely flattened light areas above anterior-most portions of M-pattern; two small, irregular-shaped dark markings on anterolateral margins between

antennal bases and labrum; labrum with two semicircular dark markings along anterior margin, two larger, faint, semicircular dark markings along posterior margin, some specimens with markings diffuse, narrowly connected; variable, flatly rounded, thin, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern; small, triangular-shaped light areas along outer lateral margins of lateral ocelli; recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows. Interocular area brown, sometimes with variable, mesoposterior light brown marking extending posteriorly from below anterior ocellus to epicranial intersection; post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction. Lacinia with 1 axilary seta, 19–24 marginal setae below subapical tooth, 11–13 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp variable, usually short indistinct row of small, vestigial denticles, occasionally distinct row of large, sharp denticles reaching about 1/2 length of inner margin (Fig. 6). Submental gills at least 2x as long as width at base. Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs; anterior transverse furrow thick, dark brown, almost black anteriorly, anterior margin light brown to brown; posterior transverse furrow thin mesally, medium to dark brown, almost black anteriorly; posterior margin brown, light lateral margins; central pronotum indistinctly patterned with two, irregular-shaped, curved brown bands on each side of mostly light colored dorsal suture, extending almost entire length of discs, these bands usually

connected centrally more than once, thus obscuring their distinctive shape, becoming more pronounced in older preserved specimens; light colored, variable-shaped, curved, light stripes radiate from anteromesal to posterolateral areas, remainder of pronotum mostly brown; anterior and lateral margins with row of stout peg-like setae, sometimes with 1–4 longer setae near corners, lateral margin setae usually similar to anterior, not interrupted near mid-length; posterior margin peg-like setae generally becoming long, stout, erect setae, long fine, silky setae near dorsal suture; pronotum covered with moderately sparse, short, clear, clothing setae. Meso-Metanota light brown, usually a large pair of mesoanterior light oval areas on each disc, sometimes single, tear-drop-shaped, with thin longitudinal dark band bisecting oval areas faded or absent in preserved specimens; long, thin, curved, posteriorly widened, light areas mesally, near dorsal suture, between mesoanterior light areas; variable heart-shaped light area along posterior half of dorsal suture. Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–8, segment one all brown except small, rounded, light area at mesoposterior margin, 9th and 10th terga with variable-shaped mesoposterior light areas, preserved specimens may appear all brown, all yellow, or sometimes with thin posterior dark bands where anterior margins lie over ventral margins; short, clear, clothing setae interspersed between stout spines; posterior margins with continuous row of spinules, those on 10th tergum single or multiple at mesoposterior margin. Posterior setal row of male 8th abdominal sternum interrupted mesally in at least mature nymphs. Cercal segments brown; apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.

Ovum. — General shape oval, triangular cross section (Fig80). Color light brown. Length 414.6–448.8 µm, width 268.3–278.0 µm. Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, with three large stabilizing carinulae at each anterior angle (Fig. 81). Chorionic surface granular (Fig. 82). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located within evenly raised, smoothly rounded, micropylar tubes (Fig. 82).

Material examined. — TYPES: *I. frontalis*, Holotype ♀, NEW YORK: Trenton Falls, River ?, Date ?, Collector ?, [Digital Photo], (BNHM). *I. hudsonicus*, Holotype ♂ and allotype ♀, HUDSON BAY TERRITORY: Ungava Bay, River ?, Date ?, L.M. Turner, (2 Slides), # 1794, (CUIC). Paratypes; *I. hudsonicus*, HUDSON BAY TERRITORY: Ungava Bay, River ?, Date ?, L.M. Turner, 1 ♀ (abdomen cleared), (NMNH), Ungava Bay, River ?, Date ?, L.M. Turner, 1 ♂, 1 ♀ (male cleared), (NMNH). NEWFOUNDLAND: Grand Lake, River ?, 28/VII/1916, Collector ?, 1 ♂, (2 Slides, 1 Vial) # 1794.3 (CUIC), Grand Lake, River ?, 25/VII/?, Collector ?, 2 ♂ (1 Slide), # 1794.4, (CUIC), Grand Lake, River ?, 1942?, Collector ?, 1 ♂ (1 Slide), # 1794.5, (CUIC), Grand Lake, River ?, Date ?, Collector ?, 1 ♂ (NMNH). ONTARIO: Location ?, Grand R., 1/VII/1888, L. Cabot, 1 ♂ (1 Slide), # 1794.2, (CUIC).

Additional specimens — *CAN*: QUEBEC: Top of Kokooak – Ungava, River ?, 8/VII/1962, Collector ?, 1 ♂ (reared?) (NMNH), Baie James, Trib. Lac Helen, 23/VI-8/VII/1975, J. Frechette, 3 ♀ (UM), Location ?, Riv. de la Mare, P.P. 20/V/1987, Harper & F. Harper, 2 Nymphs, (UM), Location ?, Trib. Nord Ouest Riv. du Gouffre, 10/IV/1987, P.P Harper & F. Harper, 1 Nymphs (UM), Hwy. 138 at Beaupre, Riviere St. Anne, 15/VI/1997, Collector ?, 1 ♀ (BYU).

LABRADOR: Churchill Falls, Churchill R., 12/VI/1979, Collector ?, 2 Nymphs (BYU), Univ. of NF Memorial near Wabash, Jean Rapids, 13/V/1980, M. Colbo & ? Larsen, 4 Nymphs (BYU), Elephant Head Lake near Wabash, River ?, 16/VI/1982, Collector ?, 1 ♀ (BYU), Minipi Drainage, Anne Marie Lake, 17/VII/1983, Collector ?, 1 ♀ (BYU), Minipi Drainage, Monipi Lake, 23/VII/1983, Collector ?, 1 ♀ (BYU), Minipi Drainage, Lower Hairy Lake, 26/VI/1983, D. Butts & D. Larsen, 1 ♀ (BYU), Wabash, Canning Lake Outlet, 6/VI/1984, ? McCradic, 3 Nymphs (BYU), Labrador City, Walsh R., 13/V/1980, Collector ?, 1 Nymph (BYU), Hwy. 530 S. of Labrador City, Walsh R., 10/VI/1997, B.C. Kondratieff & R.W. Baumann, 1 Nymph, (CSU), Hwy. 530 S. of Labrador City, Walsh R., 10/VI/1997, R.W. Baumann & B.C. Kondratieff, 2 Nymphs, (BYU), Hwy. 530 W. of Ross Bay Junction, Ashuanipi R., 12/VI/1997, B.C. Kondratieff & R.W. Baumann, 3 Nymphs (CSU), Hwy 500 W. of Ross Bay Junction, Ashuanipi R., 12/VI/1997, R.W. Baumann & B.C. Kondratieff, 5 Nymphs (BYU).

NEWFOUNDLAND: St. Anthony, River ?, Date ?, O. Bryant, 1 ♂ (NMNH), Hwy. 530 W. of Springdale, Indian Brook, 8/VI/1998, B.C. Kondratieff & R.W. Baumann, 3 ♀ (CSU), Hwy. 390 nr. Jct. w/ Hwy 1, W. of Springdale, Indian Brook, 8/VI/1998, R.W. Baumann & B.C. Kondratieff, 6 ♀ (BYU), Hwy. 1 E. of Bishops Falls, Exploits R., 9/VI/1998, R.W. Baumann & B.C. Kondratieff, 1 ♀ (BYU), Hwy. 1, South Branch Grand Codroy R., 5/VI/1998, B.C. Kondratieff & R.W. Baumann, 2 ♂ (CSU), Hwy. 1, South Branch Grand Codroy R., 5/VI/1998, R.W. Baumann & B.C. Kondratieff, 1 ♂, 2 ♀ (BYU), NE. of Cormack, Humber R., 8/VI/1998, B.C. Kondratieff & R.W. Baumann, 4 ♀ (CSU), NE. of Cormack, Upper Humber R., 8/VI/1998, R.W. Baumann & B.C. Kondratieff, 1 ♂, 1 ♀ (BYU), Hwy. 430 at Bellburns, Bound Brook, 5/VI/1998, R.W.

Baumann & B.C. Kondratieff, 1 ♂, 1 Nymph (BYU), Hwy. 1 W. of South Brook, West Brook, 9/VI/1998, B.C. Kondratieff & R.W. Baumann, 3 ♂, 1 ♀ (CSU), Hwy. 1 W. of South Brook, West Brook, 9/VI/1998, R.W. Baumann & B.C. Kondratieff, 2 ♂, 1 ♀ (BYU), Reidville Rd. N. of Deer Lake, Rocky Brook, 8/VI/1998, R.W. Baumann & B.C. Kondratieff, 2 ♀ (BYU), Indian River Camp, River ?, 13/VI/1961, M. Smith, 1 ♀ (BYU), Katherine Cove, Lake Superior, 14/VI/1974, D. Barton, 3 ♀ (NMNH), Alona Bay, Lake Superior, 16/VI/1974, D. Barton, 1 ♂, 2 ♀, 1 Nymph (NMNH), Sand Bay, Lake Superior, 19/VI/1974, D. Barton, 1 ♀ (NMNH), Kinhuron Rd. 3 mi. S. of Douglas Point, Lake Huron, 28/V/1974, D. Barton, 2 ♀ (NMNH).

USA: MICHIGAN: Benzie Co., Honor, Platte R., 27/V/1939, T.H. Frison & H.H. Ross, 1 ♂ (reared) (INHS-2467), Honor, Platte R., 27/V/1939, T.H. Frison & H.H. Ross, 1 ♂ (reared) (INHS-2469); Lake Co., Nirvana, Sanford Cr., 10/V/1940, T.H. Frison & H.H. Ross, 1 Nymph (INHS); Marquette Co., Marquette, Lake Superior, ?/?/1911, Collector ?, 1 ♀ (NMNH); Montmorency Co., Location ?, Hunt Cr., 30/VIII-3/IX/1940, J. Leonard, 1 ♂ (INHS), Location ?, Hunt Cr., 14/IV/1939, J. Leonard, 1 Nymph (INHS).

NEW YORK: County ?, Niagara Falls, River ?, June ?, Collector ?, 1 ♂, (NMNH).

WISCONSIN: Bayfield Co., Fish Cr. Rd. & Old US 2 at confluence w/ Fish Cr., Pine R., 9/IV/2000, J.B. Sandberg, S.W. Szczytko, K.W. Stewart, 10 ♂ (reared), 5 ♀ (reared), 32 Nymphs (JBS), Big Rock State Pk. NW. of Washburn, Sioux R., 9/IV/2000, J.B. Sandberg, S.W. Szczytko, K.W. Stewart, 4 Nymphs (JBS), Intersection of Carmichael & Cranberry Rds. 3 mi. S. of Herbster, East Fork Cranberry R., 8/IV/2000, J.B. Sandberg, S.W. Szczytko, K.W. Stewart, 4 Nymphs (JBS), At Siskiwitt Falls Cornucopia, Siskiwitt R., 8/IV/2000, J.B. Sandberg, S.W. Szczytko, K.W. Stewart, 1 ♀

(reared), 4 Nymphs (JBS); Douglas Co., Cty. Hwy. H 1.5 mi. N. of Brule, Rocky Run Cr., 7/IV/2000, J.B. Sandberg, S.W. Szczytko, K.W. Stewart, 9 ♂ (reared), ♀ (reared), 30 Nymphs (JBS).

Distribution. — CANADA: Labrador, Manitoba (Ricker 1964), Newfoundland, Ontario, Québec, Saskatchewan (Dosdall and Lemkuhl 1979); USA: Maine (Mingo 1983), Michigan, Minnesota (Frison 1942, Harden and Mickel 1952), New York (Hanson 1943), Wisconsin (Fig. 2).

Diagnosis and Discussion. — Males and females of *I. frontalis* are most similar to *I. colubrinus*. Males can be distinguished by the broader, sub-triangulate, lateral stylets (Fig. 72, 86). Females and nymphs cannot be reliably separated from *I. colubrinus* except by geographic distribution (Fig. 2). The transverse, anterior abdominal bands of *I. frontalis* when present (Fig. 69) are generally thicker than *I. colubrinus* (Fig. 11).

No detailed information on life history are available; observations of nymphal growth were made by Haro et al. (1994), and the drumming signals were reported by Graham (1982). Materials examined and limited laboratory rearing indicates emergence begins in mid May for Wisconsin, and continues to late July with peak emergence in June.

After examination of types of *I. hudsonicus* (Hanson 1943), from Hudson Bay Territories (locations and rivers not reported), and other materials from Wisconsin, Labrador, Newfoundland, and northern latitudes of Québec, I support Ricker's (1943) synonymy of *I. hudsonicus* (Hanson) with *I. frontalis*. This decision is based on:

1. Primary and secondary descriptions for *I. colubrinus* and *I. frontalis* were vague, relying upon variable hemitergal lobe characters for separation (Ricker 1952).

2. In 1943, Hanson placed *I. colubrinus* into synonymy with *I. frontalis* based on his assumptions that they were one, widely distributed and variable species. His illustration of *I. frontalis* lateral stylets (fig. 3, p. 667) supports our description of *I. colubrinus*.

3. Hanson's (1943) new species *I. hudsonicus* written description and illustrated ♂ lateral stylets (fig. 7, p. 667), fit our description of *I. frontalis*.

4. In 1949, Hanson again figured *I. hudsonicus* lateral stylets and variable hemitergal lobes that support our description of *I. frontalis*.

5. All *I. hudsonicus* types support our description of *I. frontalis* except for one paratype: Northwest Territories, Location ?, Great Slave Lake, Date ?, Collector?, 1 ♂ (NMNH). This male keys to *I. frontalis*, but if the meager location data are true, represents the furthest western geographic distribution for the species (Fig. 2). I assume this specimen has been mislabeled.

6. In summary, Hanson synonymized *I. colubrinus* with *I. frontalis* (Hanson 1943), using characters that describe *I. colubrinus*. He then erected *I. hudsonicus,* using characters that describe *I. frontalis* (Hanson 1943).

Isogenoides hansoni (Ricker) (Figs. 7, 88–106)

Isogenus (Isogenoides) hansoni, Ricker, 1952. Holotype ♂, Allotype ♀, Broadhead Creek, Monroe Co., PA (Illinois Natural History Survey)
Hydroperla dorata, Frison 1942 (in part)
Isogenoides dorata, Hanson 1943 (in part)
Isogenoides hansoni, Illies, 1966

Additional references: *Isogenoides hansoni*, Ricker et al. 1968 (distribution), Kondratieff and Voshell 1979, 1982, (distribution, illustrations of male head and pronotum, male and female genitalia, key to adults in Virginia), Tarter and Kirchner 1980 (distribution), Harper et al. 1991 (life cycle), Kondratieff 2004 (distribution, description, figures and key to adults).

Male. — Macropterous. Length of forewings 14–19 mm; length of body 14–20 mm. General body color brown to dark brown and black. Dorsum of head with tiny, light area along mesoanterior margin (Fig. 95); anterolateral small, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly past epicranial suture intersection, ending inside interocellar area; tiny dark brown setae absent. M-pattern raised, without setae, dark brown throughout most of pattern, beginning to fade to brown-light brown just past anterior-most portions, these blending in pigmentation with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 95). Interocellar area dark brown with dark brown pigment entering laterally and yellow entering mesoposteriorly, dark brown areas connect lateral ocelli to anterior ocellus, extending towards antennae, ending before reaching large, lateral, medium brown rugosities; dark brown areas form small X-shaped area posterior of M-pattern (Fig. 95). Antennae dark brown, with 45+/- segments, first two segments covered with dense, clear, clothing setae, segment two with few, short, erect, brown setae apically, remaining covered with partially erect, golden brown setae. Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, with almost black pigment along posterior borders; background pigmentation brown, anterior margin dark brown, posterior margin light brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then

expanded laterally inside and above the furrow (Fig. 95). Mesonotum dark brown with thin, longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe. Legs brown with transverse, dark brown, almost black band covering anterior portion of tibia, thin yellow pigment at femur-tibia joints; outside, lateral femur with densely scattered, clear, short, thin, clothing setae; without dark brown, thin, erect setae; without thin hairless streaks; preserved specimens with femur light brown, brown to dark brown on dorsum, transverse banding on femur-tibia diffuse; tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins. Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin; first three terga with variable-shaped unpigmented areas, hemitergal and subanal lobes light brown to yellow; dorsum covered with variable setation, long, clear, moderately dense, partially erect, hair-like setae on segments 1–5; long hair-like setae on segments 5–6 restricted to anterior 1/2, posterior 1/2 short, clear, clothing setae; 7th segment with short, clear, partially erect clothing setae; segments 8–9 with short clothing setae anteriorly, longer at posterior margins of dorsally expanded humps; dorsolateral humps small, variable, restricted to terga 8–9, hardly evident in dorsal view; posterolateral areas of 8th tergum slightly swollen dorsally, not laterally or posteriorly, swollen areas of tergum 8 with narrow transverse patches of slightly longer, clear, clothing setae posteriorly; 9th tergum with minutely swollen transverse lateral areas, with slightly longer clothing setae scattered posterior of hump to posterior margin (Fig. 89, 91). Sternal lobe moderate, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with

lighter brown or yellow pigment, the lightest along posterior margin, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view with lobe apices directed medially and posteriorly, apical margins broadly rounded, connected anteriorly by small, hardly visible membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 89); 10–20 light brown, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (89, 91); short, dark, erect setae scattered laterally on lobe, a few anteriorly, these interspersed within long, numerous, golden, hair-like setae concentrated along posterior margin of lobe apex. Epiproct apex in lateral view with single, stout, posteriorly and ventrally directed hook, its extension from epiproct about equal to epiproct width in lateral view (Figs. 90, 102, 103); posterior margin without pair of short, ventrally directed hooks; in lateral view, under high magnification, anterior portion of epiproct with long, apically irregular, wide, broadly round-tipped, scale-like setae, lateral margins without angled serrations (Fig. 104); anterior support sclerite trifid in anterior view, lateral and median arms shorter than base (Fig. 93), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 90, 102), median arm variable, tapered gradually to sharp pointed apex either ending before or after surpassing apices of lateral arms, usually ending just after surpassing 1/2 length of entire epiproct (Fig. 93); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portion, lateral margins approximately parallel for 3/4 length of epiproct from base, tapering gradually to narrow distal portion, joining inner posterior margin of apical hook (Fig. 92). Internal basal anchor in anterior view almost hour glass-shaped with narrowly expanded base tapering gradually to where

anterior keel-like sclerite connects, expanding laterally into tall, rounded, lateral plates (Fig. 94); long, bent, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located wide notch. Lateral stylets in lateral view with long, narrow base (Fig. 90); expanded areas widely rounded at nearly 3/4 total length from base, parts of expanded region lightly sclerotized, apical 1/4 wide, irregular-shaped at expanded region, margins parallel, then tapering gradually to narrowly rounded tips, posterior margin minutely serrate; in anterior or posterior view, stylets appear slightly wider than in lateral view (Figs. 92, 105); apical portions smoothly curved, apices directed dorsally. Paragenital plates small, situated laterally on membranous tissue surrounding epiproct, completely hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens. Subanal lobes rounded with dorsal and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate with wide U-shaped membranous notch beginning along mesal margins, reaching approximately 1/2 length from apex in posterior view; long, fine hair-like setae covering entire plate. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 97, 98); tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes; two large lobes dorsally, set between, slightly below lateral lobes (Fig. 97); two smaller lobes ventrally, between and slightly below lateral lobes, may not be fully everted, their inverted bases only visible (Fig. 98); distal, broadly rounded lobe projects slightly from margin in ventral view. Cercal segments brown, 20–22 segments, basal-most not fully sclerotized; basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments, becoming shorter and scattered on distal segments; tiny, dark, erect, setae sparse at basal 5–8 segments,

becoming more dense on distal segments; groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin; distal segments covered with short, dense, clear, partially erect clothing setae; secondary, apical constrictions sometimes present on some distal segments.

Female. — Macropterous. Length of forewings 17–18 mm; length of body 15–18 mm. General body color generally lighter, and head-pronotal pigmentation patterns similar to male. Subgenital plate moderately broad at base, its width usually less than 3/4 width of 8th sternum, produced from 1/2 to 3/4 length of 9th sternum; broadly rounded posterior margin (Figs. 96, 106); dark pigmentation mostly anterior and lateral with two, smaller dark brown markings on plate, located along anterolateral margins of plate, below mesally-angled posterior margins of abdomen, these markings enclosed by larger light and dark brown markings; mesally located, longitudinal yellow stripe variable, not always connected to posterior light margin.

Nymph. — General body color light brown with light and dark markings (Fig. 88). Antennae golden almost yellow; with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segment 1; usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 18–20; short, clear, intersegmental setae apparently absent. Dorsum of head with contrasting pigment pattern; fine, short, golden clothing setae sparsely scattered; light colored wide band forming M-pattern between antennal bases and median ocellus; anterior transverse brown band variable, usually thin, curved posteriorly at lateral margins, completely enclosing M-pattern anteriorly; anterior margin usually with narrow, laterally curved, transverse light band, brown area below enclosing

M-pattern without two light areas, sometimes open anteriorly; two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum, sometimes faded; labrum with two, small, semicircular dark markings along anterior margin; variable, flatly rounded light areas absent; large, tall, triangular-shaped light areas along outer margins of lateral ocelli, continuing laterally to antennal bases; recently preserved specimens with long, clear, silky setae in two, moderately dense, irregular-shaped patches on either side of epicranial stem suture, when present, extending from mesal patches to inner margin of eyes in irregular, moderately spaced rows, points of attachment marked by tiny yellow spots. Interocular area not completely brown, usually with variable, longitudinally narrow, oval-shaped yellow area in center; post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction, another at mesal end of occipital row; Lacinia with 1 axilary seta, 16–20 marginal setae below subapical tooth, 10–11 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandible under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually reaching beyond 1/2 length of cusp of one or both mandibles (Fig. 7). Submental gills at least 2x as long as width at base. Pronotum brown laterally with variable-shaped, central, light and dark markings; anterior transverse furrow thick, dark brown, anterior margin brown to dark brown; posterior furrow thin, dark brown, almost black posteriorly; posterior margin brown, light lateral margins; central area of pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to light brown in

preserved specimens; light colored bands, loosely assembled from smaller, curved, irregular-shaped segments directed posterolaterally, ending near mid-disc, enclosed by diffuse light brown; posterior half of discs with areas of small, curved, irregular-shaped light bands, concentrated laterally below light angled bands and mesally below brown longitudinal bands; thin remaining lateral areas brown; anterior and posterior margins with variable setation, short, stout, peg-like setae interspersed with long, moderately stout, golden setae, lateral margins with only short, peg-like setae; pronotum covered with short, densely scattered, thin, dark clothing setae, these fading to gold or clear in preserved material. Meso-Metanota light brown, usually with two pairs of mesoanterior, light, oval areas indistinct, separated by thin light brown bands; preserved specimens with thin brown band separating these areas faded, leaving dark clothing setae to indicate their original margins; two long, curved light areas border mesoanterior, light oval-areas along their inner, posterior and outer margins; heart-shaped light area along posterior half of dorsal suture absent; anterior and posterior margins marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly bowl-shaped; dark triangular bands adjacent to posterior bowl-shaped markings; Abdominal terga with distinct, dark, anterior and posterior, transverse bands on segments 1–9, anterior bands sometimes thin, partially to completely hidden by overlapping segments margin, segment 10 usually with only anterior margin dark, with variable lateral dark banding; short, clear to golden, clothing setae interspersed between stout spines; posterior margins with continuous row of stout spines, those on 10th tergum usually multiple at mesoposterior margin. Posterior setal row of male 8th abdominal sternum usually not interrupted mesally in mature nymphs. Cercal segments golden brown to dark brown;

apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.

Ovum. — General shape oval, triangular cross section (Fig. 99). Color light brown. Length 395.1 µm, width 253.6 µm. Collar with apically flanged rim, stalked with slightly elevated and irregular carinae, with 3 large stabilizing carinulae broadly connecting collar to each anterior angle (Fig. 100). Chorionic surface with dense, low globular processes (Fig. 101). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located on low, smoothly rounded micropylar knobs (Fig. 101).

Material examined. — TYPES: *I. hansoni*, Holotype ♂ and allotype ♀, PENNSYLVANIA: Monroe Co., Broadhead Cr., 23/IV/1937, P. Jennings, # 1553, (INHS). Paratypes; *I. hansoni*, NEW YORK: Schoharie Co., At Schoharie, River ?, 8/IV/1938, Collector ?, 1 ♂, #2530, (INHS). WEST VIRGINIA: Raleigh Co., At Dry Creek, Red Cr., 30/IV/1944, T. Frison & H. Ross, 3 exuviae, # 2529, (INHS).

Additional specimens — *CAN*: NEW BRUNSWICK: Location ?, Catamaran Brook, 20/VI/1994, D. Giberson, 1 ♂, 1 ♀ (BYU), Fredericton, River ?, 24/VI/1934, C. Atwood, 1 ♀ (BYU).

NOVA SCOTIA: Location ?, Baddeck North Fork, 11/VI/1983, P.P. Harper & F. Harper, 1 exuvia (MU), N. of Melford, Hwy. 105, Glenn Brook, 11/IV/1998, B.C. Kondratieff & R.W. Baumann, 1 ♂ (CSU), Big Intervale Cape Breton Highlands N.P., River ?, 17/VI/1955, D. Ferguson, 1 ♀ (BYU), Cape Breton Island, Inhabitants R., 19/IV/1956, Collector ?, 1 ♀ (BYU).

QUEBEC: Location ?, Riv. Doneaster, 26/III/1988, P.P. Harper & F. Harper, 1 Nymph (MU), Location ?, Riv. St. Anne (aval), 21/II/1987, P.P. Harper & F. Harper, 1 Nymph (MU), Location ?, Riv. Clinton, 12/IV/1988, P.P. Harper & F. Harper, 5 Nymphs (MU).

USA: CONNECTICUT: County ?, Marisfield?, River ?, 2/IV/1963, D. Kinsman, 1 Nymph (NMNH); Tolland Co., Storrs, River ?, 14/IV/1959, ? Camp, 1 Nymph (NMNH).

MASSACHUSETTS: County ?, Whately Glen, River ?, 18/V/1939, J.F. Hanson, 1 exuviae (NMNH); Hampshire Co., Middlefield?, Factory Brook, R. Needes, 4/V/1975, 4 ♂, 2 ♀ (MU), East Amherst, Fort R., 19/IV/1938, L. Barlett, 1 ♂ (NMNH), East Amherst, Fort R., 19/IV/1938, J.F. Hanson, 2 exuviae (NMNH), East Amherst, Fort R., 19/IV/1938, J.F. Hanson, 1 exuviae (NMNH), East Amherst, Fort R., 19/IV/1938, J.F. Hanson, 4 exuviae (NMNH), East Amherst, Fort R., 22/IV/1942, J.F. Hanson, 1 ♂ (INHS), East Amherst, Fort R., 22/IV/1942, J.F. Hanson, 1 Nymph (NMNH), East Amherst, Fort R., 20/IV/1942, J.F. Hanson, 2 exuviae (NMNH), East Amherst, Fort R., 30/IV/1952, J.F. Hanson, 1 ♀ (NMNH), East Amherst, Fort R., 24/IV/1952, J.F. Hanson, 1 ♀ (NMNH), East Amherst, River ?, 22/IV/1952, J.F. Hanson, 6 exuviae (NMNH), East Amherst, Fort R., 23/IV/1952, J.F. Hanson, 1 ♀ (NMNH).

NEW YORK: Delaware Co., 1 mi. W. of Horton, Beaver Kill R., D. Funk & J. Pierson, 27/IV/1982, 1 ♀ (reared) (DF), 1 mi. W. of Horton, Beaver Kill R., D. Funk & J. Pierson, 27/IV/1982, 2 ♀ (reared) (DF), 1 mi. W. of Horton, Beaver Kill R., D. Funk & J. Pierson, 2/V/1982, 1 ♂(reared), 1 ♀ (reared) (DF), 1 mi. W. of Horton, Beaver Kill R., D. Funk & J. Pierson, 9/V/1982, 1 ♀ (reared) (DF), 1 mi. W. of Horton, Beaver Kill R., D. Funk & J. Pierson, 9/VII/1982, 1 ♂ (reared) (DF).

PENNSYLVANIA: County ?, Ole Bull Camp Site, River ?, 9/V/1975, N. Hynes, 1 ♀, 3 exuviae (NMNH); Clinton Co., Location ?, North Fork Tangascootack Cr., 7/III/1984, 2 Nymphs (JE); Forest Co., 41º35'18"N / 79º02'57"W, 10/V/1995, E. Masteller & B. Shaffer, 3 ♀ (NMNH), Hwy. 227 NW. of West Hickory, West Hickory Cr., 22/IV/1979, 2 ♂ (BYU); Huntington Co., Near McAleveys Fort, Standing Stone Cr., 30/I/1953, Collector ?, 1 Nymph (BYU); Potter Co., Near Oleona Rt. 44, Kettle Cr., 4/V/1995, E.C. Masteller, 1 ♀ (CSU); Somerset Co., Kooser State Pk., Stream ?, 19/III/1975, R.W. Baumann & O. Flint, 2 Nymphs (UNT), Kooser State Pk., Stream ?, 19/III/1975, R.W. Baumann & O. Flint, 1 ♂ (BYU).

TENNESSEE: Blount Co., 100 m above Abrams Creek-Cades Cove-Great Smoke Mountains N.P., Mill Cr., 2/IX/1995, 7 Nymphs (DE); Sevier Co., At Gatlinburg, River ?, 2/IV/1941, J.F. Hanson, 1 ♀ (NMNH), Gatlinburg, River ?, 3/IV/1941, J.F. Hanson, 2 exuviae (NMNH), Gatlinburg, River ?, 2/IV/1941, J.F. Hanson, 1 ♀ (NMNH), Gatlinburg, River ?, 2/IV/1941, J.F. Hanson, 1 ♂ (NMNH), Gatlinburg, River ?, 2/IV/1941, J.F. Hanson, 2 exuviae (NMNH); Unicoi Co., Tennessee R. Drainage-a tributary to Indian Creek, Sams Cr., 29/XI/1995, 7 Nymphs (DE).

VERMONT: County ?, Location ?, Starksboro Cr., Collector ?, 5/I/1938, 1 Nymph (NMNH); County ?, Bellow Falls Prison Hollow, Collector ?, 5/I/1938, 1 Nymph (NMNH).

VIRGINIA; Giles Co., Pembroke Rt. 460, Little Stony Cr., 16/IV/1980, B.C. Kondratieff, 3 ♂ (reared), 10 ♀ (reared), 2 Nymphs, 10 exuviae (CSU), Pembroke Rt. 460, Little Stony Cr., 16/III/1983, B.C. Kondratieff, 3 ♀, 2 Nymphs, 1 exuvia (BYU), 2 mi. N. of confl. w/ Laurel Branch CR 635, Stony Cr., 24/II/2001, J.B. Sandberg, 1 Nymph

(JBS), 2 mi. N. of confl. w/ Laurel Branch CR 635, Stony Cr., 27/II/2001, J.B. Sandberg, B.C. Kondratieff, R.F. Kirchner, 4 ♂ (reared), 21 Nymphs (JBS).

WEST VIRGINIA: Nicholas Co., 6 mi. W. of Richwood Rt. 39, Panther Cr., 5/II/1983, R.F. Kirchner & B.C. Kondratieff, 4 Nymphs (UNT).

Distribution. — CANADA: New Brunswick, Nova Scotia, Québec; USA: Connecticut, Maine (Mingo 1983), Maryland (Ricker 1952, Duffield and Nelson 1990), Massachusetts, New York, North Carolina (Ricker 1952), Pennsylvania, Virginia, West Virginia (Fig. 2).

Diagnosis and Discussion. — Adult males of *I. hansoni* are most similar to *I. colubrinus* and *I. frontalis*. Males and females can be distinguished primarily by the thin, longitudinal, yellow pigment band entering the interocellar area from the posterior of head (Fig. 95). Males can also be separated by the length of the apical hook's extension from the epiproct and the posterior margin of epiproct without a pair of ventrally directed hooks (Fig, 90). Females can also be differentiated from *I. olivaceus* by subgenital plate's posterior margin broadly rounded, without a mesoposterior emargination. Nymphs can be separated by the thicker M-pattern of head, ventral basal margin of distal-most cusp with long row of large denticles on one or both mandibles, and dorsal, abdominal segments with anterior and posterior dark bands usually on segments 1–9.

No life history or biological studies have been done. Based on material examined and laboratory rearing, emergence begins in late April, and continues to until early July, with peak emergence in late April to early June.

Isogenoides olivaceus (Walker) (Figs. 8, 107–125)

Perla (Isogenus) olivacea Walker, 1852. Holotype ♀, St. Martin's Falls, Albany River, Ontario (British Natural History Museum)
Perla sulcata Provancher, 1876. Syn. Ricker, 1952
Perla olivacea, Claassen, 1940
Isogenus olivacea, Ricker, 1938
Hydroperla olivacea, Frison, 1942
Isogenoides olivaceus, Hanson, 1943
Isogenus (Isogenoides) olivaceus, Ricker, 1952
Isogenoides olivaceus, Illies, 1966

Additional references: Ricker 1938 (description of male/female genitalia), Ricker et al. 1968 (distribution), Hilsenhoff & Billmyer 1973 (nymph and adult keys), Hitchcock 1974 (description of male and adult key), Harper and Ricker 1994 (distribution), Kondratieff 2004 (distribution, description, figures and key to adults).

Male. — Macropterous. Length of forewings 13–15 mm; length of body 15–16 mm. General body color brown to dark brown and black. Dorsum of head with mesoanterior margin brown to light brown (Fig. 114); anterolateral irregular-shaped light areas variable, when present, small, between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow area with base along posterior margin of head, extending mesoanteriorly forming slightly truncated area, a second lateral, angled area below posterior margin of eye; tiny dark brown setae absent. M-pattern raised, without setae, dark brown throughout most of pattern, pattern not fading or blending into light brown or light anterolateral areas of frons; distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 114). Interocellar area brown variable, usually brown with dark brown pigment entering laterally and light brown median stripe, dark brown irregular-shaped areas connecting lateral ocelli to anterior ocellus variable, extending directly to large, lateral, medium brown rugosities, or sometimes anteriorly to posterior margin of M-pattern; dark brown areas usually form two short, posterolaterally directed bands, or sometimes two wide,

slightly angled, longitudinal bands connecting to inner legs of M-pattern (Fig. 114). Antennae dark brown, with 46+/- segments, covered with dense, clear, partially erect, clothing setae and sparsely scattered, short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, sometimes filled with slightly darker brown, almost black pigment along posterior borders; background pigment, anterior and posterior margins brown to light brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 114). Mesonotum dark brown with thin, longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe. Legs brown with transverse, dark brown, almost black band covering anterior portion of tibia, thin yellow pigment at femur-tibia joints; outside, lateral femur with densely scattered, clear, short, thin, clothing setae; without dark brown, thin, erect setae; with 1–2 variable length, thin hairless streaks on outer surface; tibia with dense clothing setae and scattered, erect, golden spines evenly distributed in moderately spaced longitudinal rows on posterior and inner, lateral margins; distal portion of tibia with short, thin, raised carinae below transverse dark band; Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin; first tergum with variable-shaped unpigmented areas, dorsal areas of terga 7–9, hemitergal and subanal lobes with some light brown to yellow pigment; dorsum entirely covered with long, clear, moderately dense, clothing setae; posterior margin of 8th tergite with longer, partially erect clothing

setae. dorsolateral humps small, variable, usually restricted to terga 7–8, visible in dorsal view; posterolateral areas of 7th – 8th terga slightly swollen dorsally, rarely laterally, not posteriorly, swollen areas of 8th tergite largest, sometimes with thin transverse dorsal yellow marking near posterior margin; narrow transverse patches of partially erect clothing setae along posterior margin of hump (Fig. 108, 109). Sternal lobe moderate, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with lighter brown or yellow pigment, the lightest along posterior margin, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view with lobe apices directed medially and slightly posteriorly, apical margins broadly rounded, connected anteriorly by moderately large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 109); 38–42 reddish-brown, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 108, 109); short, dark, erect setae sparse on posterior membranous portion, these interspersed within long, numerous, golden, hair-like setae covering entire posterior areas; 10th sternite dark brown. Epiproct apex modified in lateral view with double, stout anteriorly and ventrally directed hooks, their anterior extension from epiproct less than epiproct width in lateral view (Figs. 110, 121, 122); posterior margin with single, curved, long, lash-like, dorsally directed process, its position from apex about 1/3 total epiproct length in lateral view; in lateral view, under high magnification, anterior portion of epiproct with long, apically irregular, wide, variably-tipped, scale-like setae, apical tip pointed, broad to narrowly bifurcate, or multiple serrated (Fig. 123); anterior support sclerite modified in anterior view, median arm wide, attached to base normally, lateral arms separated from median arm,

extending dorsally to where they connect to ventral margins of double apical hooks (Figs. 112); posterior support sclerite modified, stout, wide at base, extending dorsally and laterally, forming partially membranous plate with two apical, small, sclerotized dorsolateral margins that partially occlude posterior portions of lateral stylets, base with irregular hole slightly more dorsal than normal, dorsal portion of anterior support sclerite modified, projecting posteriorly and dorsally away from membranous epiproct, tabular sclerite curls posteriorly and anteriorly forming progressively smaller coil (Fig. 111). Internal basal anchor in anterior view with narrowly expanded base tapering gradually to where anterior keel-like sclerite connects, expanding laterally into small, pointed, lateral plates (Fig. 113); long, slightly curved, wing-like triangular sclerites dorsal-most, directed laterally from centrally located narrow notch. Lateral stylets in lateral view with long, narrow base (Fig. 110); expanded areas widely rounded at nearly 3/4 total length from base, apical 1/4 wide, irregular-shaped at expanded region, margins tapering gradually and curves posteriorly to sharply pointed tip; in anterior or posterior view, stylets appear slightly wider in than in lateral view (Figs. 121, 136); apical portions smoothly curved, apices directed slightly laterally. Paragenital plates small, thin, situated laterally on membranous tissue surrounding epiproct, mostly hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens. Subanal lobes rounded with dorsal and posteriorly directed lobe, membranous along its dorsal and posterior margins, sclerotized plate with wide U-shaped membranous notch, reaching approximately 3/4 length from apex in posterior view; long, fine hair-like setae covering entire plate. Aedeagus membranous with pair of distinct lateral lobes slightly below dorsolateral apical margins (Figs. 108, 109); two smaller lobes located and directed

dorsally on aedeagus, situated between lateral lobes (Fig. 109); tiny, clear, erect setae sparsely scattered over entire surface of small, dorsally directed lobes; one wide, low, rounded knob located mesally and apically as seen in dorsal view. Cercal segments brown, 20–24 segments, basal-most not fully sclerotized; basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments, becoming shorter and scattered on distal segments; tiny, dark, erect, setae apparently absent; groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin; distal segments covered with short, dense, clear, partially erect clothing setae;

Female. — Macropterous. Length of forewings 16–18 mm; length of body 17–20 mm. General body color generally lighter, and head-pronotal pigmentation patterns similar to male. Subgenital plate moderately broad at base, its width usually less than 3/4 width of 8^{th} sternum, produced from 1/2 to 2/3 length of 9^{th} sternum, broadly rounded posterior margin with variable mesoposterior emargination from broad and shallow to narrow and moderately deep (Figs. 111, 124); dark pigmentation variable, from covering entire plate to patterned, with most dark pigment anteriorly and laterally with posterior margin light; two variable, large, darker markings located anterolaterally on plate, usually connected to anterior segment by two thick, brown longitudinal bands.

Nymph. — General body color light brown with light and dark markings (Fig. 107). Antennae golden almost yellow; with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segment 1; usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 13–15; short, clear, intersegmental setae apparently absent.

Dorsum of head with contrasting pigment pattern; fine, short, clear, clothing setae sparse; light colored narrow band forming M-pattern between antennal bases and median ocellus; anterior transverse brown band variable, usually thick, completely enclosing M-pattern anteriorly, becoming light brown or speckled with small yellow blotches along anterior margin; anterior margin usually with narrow, transverse light band, brown area below enclosing M-pattern without two light areas; two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum, sometimes faded; labrum with two, small, semicircular dark markings along anterior margin; variable, flatly rounded, sometimes broadly U-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern, these sometimes partially connected to variable, small, triangular light areas along outer margins of lateral ocelli, sometimes large; recently preserved specimens with long, clear, silky setae in two, sparse, irregular-shaped patches on either side of epicranial stem suture, reaching anterolaterally to inner margin of eye in widely spaced irregular row and posteriorly to mesal end of occipital spinulae row, points of attachment marked by tiny yellow spots. Interocular area brown, similar to adjacent areas; post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction, another at mesal end of occipital row; Lacinia with 1 axilary seta, 15–17 marginal setae below subapical tooth, 3–5 submarginal setae sparsely scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp with short, indistinct row of small, vestigial denticles sometimes reaching beyond 1/2 length of cusp of one or both mandibles (Fig. 8). Submental gills short, at most 2x

as long as width at base. Pronotum brown laterally with variable-shaped, central, light and dark markings; anterior transverse furrow thick, dark brown; posterior transverse furrow thin, dark brown, almost black on posterior border; anterior and posterior margins brown, lateral margins light; central area of pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to light brown in preserved specimens; variable, diffuse, light brown bands formed from smaller, curved, irregular-shaped segments radiate outwards, posterolaterally on central areas of each disc, enclosed by diffuse light brown; lateral and posterior areas of discs with variable-shaped, elongate, light stripes, remaining pronotum with various brown and light brown areas, on preserved specimens light colored stripes connected, additional stripe continuing towards anterior mesal area, forming irregular trapezoid shaped band over center of pronotum; pronotal marginal setae variable, long silky setae mesally at anterior and posterior margins near dorsal suture; anterior and posterior setae becoming long, stout, erect, golden setae with short, peg-like setae interspersed, continuing to lateral margins, sometimes with 1–4 longer setae near corners; lateral margins with variable setation, from all short peg-like to interspersed with long, erect setae; pronotum covered with densely scattered, short, thin, clear clothing setae. Meso-Metanota light brown, usually with one pair of mesoanterior, light, oval areas indistinct, usually partially filled with light brown; two long, curved, posteriorly widened, light areas border larger, light, oval areas along mesoposterior inner, margins; a central pair of long, wide, anteriorly curved light bands positioned laterally posteriorly to mesoanterior oval areas; posterior heart-shaped light areas absent; anterior and posterior margins

marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly bowl-shaped; faded brown triangular-shaped bands adjacent to posterior bowl-shaped markings present or absent; Abdominal terga with distinct, dark, anterior and posterior, transverse bands on segments 2–9, segment one with posterior transverse band thin, often faded in preserved material; segment 10 with dark pigment variable, sometimes with a pair of median yellow transverse bands with some dark pigment near posterior margin; short, clear, clothing setae sparsely interspersed between stout spines; posterior margins with continuous row of stout spines, those on 10th tergum usually multiple at mesoposterior margin. Posterior setal row of male 8th abdominal sternum usually not mesally interrupted or with short interruption in mature nymphs. Cercal segments golden brown to dark brown; apical whorl of short, stout setae, those located at mesoposterior apical margin becoming longer on distal segments.

Ovum. — General shape oval, triangular cross section (Fig. 118). Color light brown. Length 409.7 µm, width 282.9 µm. Collar with slight apically flanged rim, stalked with slightly elevated and irregular carinae, apical margin deeply incised between 3 large stabilizing carinulae that broadly connect to collar at each anterior angle (Fig. 119). Chorionic surface granular (Fig. 120). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located on long, irregular micropylar tubes (Fig. 120).

Material examined. — TYPES: *I. olivaceus*, Holotype ♀, ONTARIO: St. Martin's Falls, Albany R., Date ?, Collector ?, [Digital Photo], (BNHM).

Additional specimens — *USA*: MICHIGAN: Dickinson Co., T43N, R29W, S11, 12/XII/1983, J. Stout & R. Merritt, 1 Nymph (UNT); Lake Co., Hwy. 37 bridge, Pere

Marquette R., 10/IV/1999, J.B. Sandberg & B.C. Kondratieff, 2 ♂ (reared), 1 ♀ (reared) (JBS), Hwy. 37 bridge at Forks, Pine R., 10/IV/1999, J.B. Sandberg & B.C. Kondratieff, 1 ♂ (reared) (JBS), Walker's Bridge, Pine R., 10/IV/1999, J.B. Sandberg & B.C. Kondratieff, 6 ♀ (reared), 4 Nymphs (JBS); Otsego Co., Location ?, Pigeon R., 1/IV/1989, R. Haro, 4 Nymphs (RH).

WISCONSIN: Florence Co., Hwy 101, Woods Cr., 23/IV/1987, M.T.Z., 1 ♂ (BYU); Langlade Co., Cty. Hwy. HH bridge, South Branch Oconto R., 9/IV/1992, J.B. Sandberg, J.J. Dimick, S.W., Szczytko, 1 ♂, 1 ♀, 4 Nymphs (JBS).

Distribution. — Distribution. — CANADA: Ontario (Harper and Ricker 1994), Québec (Ricker et al. 1968); USA: Michigan, Minnesota (Stark et al. 1986), Pennsylvania (Stewart and Stark 2002), Wisconsin (Fig. 2).

Diagnosis and Discussion. — The male epiproct distinguishes this species from all the *Isogenoides* (Fig. 110). Females are most similar to *I. doratus* and can be tentatively separated by their slightly more narrow subgenital plate (Fig. 115). The posterior margin is slightly emarginated and this character is shared with *I. doratus* (Fig. 39), which may present difficulty when attempting to identify these species from areas with overlapping geographic distribution (Michigan and Québec). Mature male nymphs are easily separated by the presence of large developing epiproct (Fig. 107) and late instar female nymphs can be separated tentatively by the ventral basal margin of distal-most cusp with small (vestigial) denticles on one or both mandibles (Fig. 8), and dorsal, abdominal segments with anterior and posterior dark bands usually on segments 1–9 (Fig. 107).

No life history studies have been done. An unpublished master's thesis included this species in descriptions of Wisconsin stonefly drumming (Ziminske 1989). Based on the material examined, emergence occurs in April.

Isogenoides varians (Walsh) (Figs. 9, 126–144)

Perla varians Walsh, 1862. Lectotype ♂ design. Hanson, 1943, Rock Island, IL (Museum of Comparative Zoology)
Perla varians, Needham and Claassen, 1925
Hydroperla varians, Frison, 1935
Hydroperla varians, Frison, 1937
Isogenoides varians, Hanson, 1943
Isogenus (Isogenoides) varians, Ricker, 1952
Isogenoides varians, Illies, 1966

Additional references: Ricker 1945 (distribution), Harden & Mickel 1952 (state that their only known record was given by Needham & Claassen (1925), Hitchcock 1974 (description and adult key), Kondratieff and Kirchner 1987, 2004 (distribution), Kondratieff et al. 1995 (distribution), Kondratieff 2004 (distribution, description, figures and key to adults).

Male. — Macropterous. Length of forewings 13–15 mm; length of body 15–17 mm. General body color brown to dark brown and black. Dorsum of head with variable, tiny, light area along mesoanterior margin (Fig. 133); anterolateral large, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow area with base along posterior margin of head, anterolateral borders angled posteriorly, sometimes pointed, where broadly rounded mesoanterior border extends almost to epicranial suture intersection; tiny dark brown, erect setae, sparsely scattered on light or yellow pigment areas. M-pattern raised, without setae, dark brown throughout most of pattern, pattern not fading or blending into light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 133). Interocellar area generally medium brown with dark brown pigment entering laterally, dark brown

areas connect lateral ocelli to anterior ocellus, extending directly to large, lateral, medium brown rugosities; dark brown areas form two short, posterolaterally directed bands (Fig. 133); Antennae dark brown to black, with 43+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden brown setae. Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, anterior furrow with short, thin almost black sutures along mesoposterior border; posterior furrow with dark brown almost black pigment along posterior border; background pigment, anterior and posterior margins brown to light brown; clothing setae short, densely scattered with small yellow spots at attachment points, a few partially erect, short, dark setae interspersed among these. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to anterior margin of anterior transverse furrow, then expanded laterally above furrow (Fig. 133). Mesonotum dark brown with variable longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe. Legs brown, with short, transverse dark brown, almost black band covering tibia-femur joint, femur with dark pigment continuing as thin dorsal stripe to base, thick yellow pigment at femur-tibia joint; outside, lateral femur with densely scattered, clear, short, thin, clothing setae; without dark brown, thin, erect setae; with 1–2 variable length, thin hairless streaks on outer surface; tibia with dense clothing setae and scattered, erect, golden spines evenly distributed in moderately spaced longitudinal rows along posterior margins. Abdomen dark brown without thin dark brown to black transverse stripes along anterior margins; first tergum with variable-shaped unpigmented areas, hemitergal and subanal lobes yellow in dorsal view,

contrasting sharply with darker cerci; dorsum entirely covered with dense, short, clear to light brown, clothing setae, longer at mesoposterior areas of terga 8–9, those on 8 longest; dorsolateral humps small, restricted to terga 8–9, visible in dorsal view, posterolateral areas slightly swollen dorsally, not laterally or posteriorly, swollen areas of 8th tergite largest; 9th tergite with variable transverse light area; wide transverse patches of partially erect clothing setae cover dorsal areas of humps (Figs. 127, 128). Sternal lobe large, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with yellow pigment, posterior margin not extending past posterolateral margins of 7th sternite. Hemitergal lobes in dorsal view with lobe apices directed posteriorly, not medially or anteriorly, apical margins narrowly rounded to slightly pointed, connected anteriorly by tiny, thin, laterally extended membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 128); 14–20 wide, mostly short, golden brown, stout spinulae (sensilla basiconica) concentrated along mesoanterior margins of sclerites (Figs. 127, 128); short, dark, erect setae scattered over entire posterior portion of lobe, these interspersed within long, numerous, golden, hair-like setae covering entire posterior areas; 10th sternite with small variable dark pattern. Epiproct apex modified in lateral view with deep, internally sclerotized groove, not a hook (Figs. 129, 140, 141); posterior margin with heavily sclerotized pair of long, basally broad, posteriorly directed hooks, their position from apex about 1/5 to 1/6 total epiproct length in lateral view; in lateral view, under high magnification, anterior portion of epiproct with long, apically curved or slightly expanded, bluntly tipped, scale-like setae, lateral margins with deep, angled serrations (Fig. 142); anterior support sclerite trifid in anterior view, lateral arms stout, longer than base (Fig. 131), in lateral view

curved anteriorly at apex with apical, anterior expansions forming thin, hook-like processes (Figs. 129, 140, 141), median arm separated from lateral arms basally, its apically pointed dorsal portion as long as base, ending before 1/2 length of entire epiproct (Fig. 131); posterior support sclerite single, stout, wide, lateral margins approximately parallel, with irregular-shaped hole near base below membranous epiproct portion, lateral margins expanding sharply to join laterally at slightly more than 3/4 total epiproct length from base, to pair of stout, heavily sclerotized, inwardly and posteriorly directed hooks, support sclerite continuing dorsally, margins parallel then tapering sharply, connecting to broad, apical, sclerotized groove (Fig. 130); Internal basal anchor in anterior view with narrowly expanded base tapering gradually to where anterior keel-like sclerite connects, expanding gradually into broadly triangular lateral plates (Fig. 132); long, wide, slightly curved, wing-like triangular sclerites dorsal-most, directed dorsally from centrally located wide notch. Lateral stylets in lateral view with long, wide base (Fig. 129); expanded areas narrowly rounded at slightly more than 1/2 total length from base, apical 1/2 narrow at expanded region, margins approximately parallel, curving slightly to broadly rounded tips; in anterior or posterior view, stylets appearing about as wide as in lateral view (Figs. 130, 143); apical portions smoothly curved, apices directed slightly laterally. Paragenital plates large, with distinct longitudinal carinae, situated laterally on membranous tissue surrounding epiproct, mostly hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted males. Subanal lobes rounded with dorsal and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate covering approximately 1/2 length of entire lobe with wide U-shaped notch beginning along mesal margin, reaching

3/4 length from apex in posterior view; long, fine hair-like setae covering entire plate. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 135, 136); tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes; two wide lobes dorsally, set between, slightly below, lateral lobes (Fig. 135); two plate-like lobes ventrally, immediately below lateral lobes (Figs. 1A, 127), may not be fully everted in some specimens, their inverted bases only visible (Fig. 136), dorsal apex sometimes bearing globular, fixed extruded semen appearing as additional lobes (Figs. 1A, 127); one low, moderately projected rounded knob, located mesally and apically as seen in dorsal view. Cercal segments dark brown, 25–27 segments, basal-most not fully sclerotized; basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments, becoming shorter and scattered on distal segments; tiny, dark, erect, setae apparently absent; groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin; distal segments covered with shorter, less dense, brown, partially erect clothing setae.

Female. — Macropterous. Length of forewings 16–18 mm; length of body 17–20 mm. General body color and head-pronotal pigmentation patterns similar to male. Subgenital plate broad at base, its width usually greater than 3/4 width of 8th sternum, produced from 3/4 to entire length of 9th sternum; broadly rounded posterior margin with variable mesoposterior characters (Figs. 134, 144): 1. mesoposterior margin of subgenital plate with short, almost vestigial, wide protrusion, 2. mesoposterior margin of subgenital plate with short, almost vestigial, narrow to wide, emarginated protrusion, 3. posterior margin of subgenital plate entire; 5 dark pigmentation variable, from covering entire plate to patterned, sometimes with two, small, rounded light markings on plate,

below mesally angled, posterior margins of abdomen, these markings enclosed by dark pigment posteriorly, connected to two, wide, light brown to yellow, longitudinal bands on anterior portion of segment.

Nymph. — General body color yellow with light and dark markings, yellow fading to cream when preserved (Fig. 126). Antennae yellow to cream; with short, erect, golden peg-like setae arranged as whorls around apical margins, segment one with scattered, long, dark clothing setae, these fading to clear when preserved; usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 17–19; short, clear, intersegmental setae apparently absent. Dorsum of head with contrasting dark pigment pattern when live or recently preserved, becoming faded over time to light tan patterns mostly on posterior half; long dark clothing setae scattered mostly over pigmented areas; light colored narrow band forming M-pattern between antennal bases and median ocellus partially enclosed with dark pigment, its margins indicated by presence of long, dark moderately scattered, clothing setae enclosing pattern; anterior transverse brown band reduced, narrow, following contour of anterior M-pattern margin, usually faded on preserved specimens; anterior margin largely yellow to unpigmented, 4 small, irregular shaped dark markings mesoanteriorly between antennal bases and labrum, brown band below without two light areas; one pair located mesally above anterior-most portions of M-pattern, all mostly faded in preserved material; labrum usually yellow to unpigmented, covered with long, dark clothing setae; variable, flatly rounded, light areas absent; large, nearly triangular light areas above lateral ocelli, extending to median ocellus, laterally to inner margin of eye, anterior margins enclosed by thin, irregular-shaped, transverse brown band below M-

pattern, this extending to anterior, inner margin of eyes; recently preserved specimens with few, long, clear, silky setae in two, irregular, sparse patches near mesal portions of occipital spinule row. Interocular area brown, partially faded when preserved; post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction. Lacinia with 1 axilary seta, 15–18 marginal setae below subapical tooth, 9–11 submarginal setae sparsely scattered from below apical tooth downwards to base. Left and right mandibles under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually extending beyond 1/2 length of cusp of one or both mandibles (Fig. 9). Submental gills at least 2x as long as width at base. Pronotum mostly yellow to unpigmented with variable-shaped, central, light and dark markings; long dark, clothing setae moderately dense, covering mostly pigmented areas; anterior transverse furrow thick, dark brown, anterior margin light to dark brown; dark to light brown short, broadly rounded markings connected to posterolateral, anterior furrow borders; posterior furrow variable, generally thick with thin section near dorsal suture curving posteriorly, filled with dark brown; posterior margin light brown, lateral margins light; dark to light brown variable, rounded markings connected to anterolateral and mesoanterior borders of posterior furrow; central area of pronotum indistinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to speckled light tan in preserved specimens and are covered with long, dark, clothing setae; one long, distinctly curved, longitudinal light stripe on outer lateral margins of median dark bands, followed by three, indistinct, loosely assembled light

bands, formed from smaller, curved, irregular shaped segments, these directed posterolaterally, ending near mid-disc, enclosed by diffuse, light tan; long, lateral, dark bands begin narrowly below lateral portions of anterior furrows, expanding posteriorly at posterior corners of discs; anterior and lateral margins with short, stout, peg-like setae, posterior margin with peg-like setae becoming longer mesally; pronotum covered with long, moderately dense, dark clothing setae. Meso-Metanota yellow to cream when preserved, usually with two pairs of mesoanterior, light oval areas indistinctly separated by thin, light brown to tan bands; a short thin pair centrally, along dorsal suture, and a large, thick, light area lateral of mesoanterior pair; posteriorly, with a wide, short, light oval area near dorsal suture, separated from large, thick light area laterally with thin light brown to tan stripe; posterior heart-shaped area absent; anterior and posterior margins marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly, bowl-shaped, open mesoposteriorly; brown, triangular-shaped bands adjacent to posterior bowl-shaped markings faded. Abdominal terga when recently preserved, with distinct, dark, anterior, transverse bands on segments 1–10, first and 10^{th} segments with bands completely faded after 7-months in 75% EtOH; long, dark, clothing setae sparsely interspersed between stout spines; posterior margins with continuous row of stout spines, those on 10^{th} tergum usually in single, approximately linear row. Posterior setal row of male 8^{th} abdominal sternum variable, from not mesally interrupted to short interruption in mature nymphs. Cercal segments yellow; apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.

Ovum. — General shape oval, triangular cross section (Fig. 137). Color yellow. Length 414.6 µm, width 253.6 µm. Collar with slight apically flanged rim, stalked with irregularly concentrated, small, globular processes, and with 3 large stabilizing carinulae broadly connecting to collar at each anterior angle (Fig. 138). Chorionic surface mostly smooth, with granular processes concentrated and largest on angles (Fig. 139). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located below short, smooth, elevated, cup-like sperm guides (Fig. 139).

Material examined. — TYPES: *I. varians*, Lectotype ♂, ILLINOIS: Rock River, Rock Island, [not at MCZ]; Syntypes 2♀♀, ILLINOIS: Rock River, Rock Island, Date ?, Collector?, (both pinned), # 10128, (MCZ).

Additional specimens — *USA*: INDIANA: Tippecanoe Co, W. Lafayette, (Wabash R.?), 26/IV/1959, Collector ?, 1 ♂ (BYU); Pike Co., Rodgers, White R., 30/IV/1936, Collector ?, 1 exuvia (INHS), Petersburg, White R., 30/IV/1936, Mohr & Burks, 1 exuvia (INHS), Rogers, White R., 21/IV/1936, T.H. Frison & Mohr, 1 exuvia (INHS), Rogers, White R., 21/IV/1936, T.H. Frison & Mohr, 1 Nymph (INHS), Rogers, White R., 16/IV/1936, H.H. Ross & Mohr, 2 ♂ (reared) (INHS).

ILLINOIS: Pope Co., Golconda, Ohio R., 19/IV/1914, Collector ?, 1 ♂ (INHS); Wabash Co., Mt. Carmel, Wabash R., 8/IV/1939, T.H. Frison & Burks, 2 ♂ (INHS), Mt. Carmel, Wabash R., 8/IV/1939, T.H. Frison & Burks, 2 ♂ (INHS), Mt. Carmel, Wabash R., 8/IV/1939, T.H. Frison & Burks, 2 ♂, 1 ♀ (INHS), Mt. Carmel, Wabash R., 8/IV/1939, T.H. Frison & Burks, 1 Nymph (INHS).

MISSISSIPPI: Simpson Co., Hwy 472, Mill Cr., 10/II/1986, B.P. Stark, 2 Nymphs (BPS), Hwy. 472, 4 mi. S. of Pinola, Mill Cr., 28/II/1981, B.P. Stark & M. Britton, 3

exuviae (BPS), Hwy. 472, 4 mi. S. of Pinola, Mill Cr., 28/II/1981, B.P. Stark & M. Britton, 4 ♂, 2 ♀ (BPS), Hwy. 472, 4 mi. S. of Pinola, Mill Cr., 16/I/1981, B.P. Stark, 1 Nymph (UNT), Hwy. 43, Westville Cr., 1/24/2001, C. Simpson, 2 Nymphs (BPS), Hwy 43 at Pinola, Westville Cr., 12/II/2000, J.B. Sandberg, B.P. Stark, K.W. Stewart, 7 ♂ (reared), 5 ♀ (reared), 9 nymphs (JBS), Hwy 43 at Pinola, Westville Cr., 30/I/2004, J.B. Sandberg, B.P. Stark, K.W. Stewart, 4 ♂ (reared), 7 ♀ (reared), 12 nymphs (JBS).

SOUTH CAROLINA: Pickens Co., River ?, 26/III/1929, Collector ?, 1 ♂ (INHS).

TENNESSEE: Sevier Co., Greenbriar Cove Great Smoky Mountains N.P., River ?, June-July 1940, A. Cole, 1 ♂ (INHS).

VIRGINIA: Bedford Co., 11 mi. SE. of Bedford, Rt. 24, Big Otter R., 7/XI/1983, B.C. Kondratieff & R.F. Kirchner, 2 Nymphs (UNT), Hwy. 24 bridge, Big Otter R., 26/II/2001, 4 ♂ (reared), 2 ♀ (reared), 6 Nymphs (JBS).

Distribution. — USA: Illinois, Indiana (Ricker 1945, Grubbs 2004), Kansas (Needham and Claassen 1925), Michigan (Needham and Claassen 1925, Hanson 1943), Minnesota (Needham and Claassen 1925), Mississippi, North Carolina (Kondratieff and Kirchner 2004), South Carolina, Tennessee, Virginia (Fig.2).

Diagnosis and Discussion. — The male epiproct is diagnostic with an apically sclerotized groove (Fig. 129). The posterior epiproct margin has a pair of stout, heavily sclerotized, posteriorly directed hooks (Fig. 141) which is a shared character with *I. doratus* (Fig. 34) and *elongatus* (Fig. 53). Females are generally closest to *I. doratus* and *olivaceus* with subgenital plate posterior margins broadly rounded; *I. varians* can tentatively be separated from these by subgenital plate being produced from 3/4 to entire length of the 9th sternum (Fig. 134). Nymphs in alcohol are light yellow to

unpigmented and can be separated by having large denticles along inner, ventral margin of the distal-most mandibular cusp (Fig. 9), abdominal terga with one anterior transverse band (Fig. 126), and dorsum with long, dark, clothing setae.

No life history or biological studies have been done. Based on our laboratory rearing and material examined, emergence begins in February, and continues through April, with peak emergence probably in early March. Needham and Claassen (1925) reported this species from Kansas, Michigan, and Minnesota, however, no museum, other personal holdings, or other published reports support these distributions. Hanson (1943) reported two females from Port Huron, Michigan (CUIC, MCZ), which were probably *I. olivaceus*.

Isogenoides zionensis Hanson (Figs. 10, 145–163)

Isogenoides zionensis Hanson, 1949. Holotype ♂, Zion National Park, UT (Smithsonian National Museum of Natural History)
Isogenoides zionensis, Illies 1966

Additional references: *Isogenoides zionensis*, Gaufin, 1955; Ricker 1955 (Northwest Territories collection record); Ricker 1964 (possible greatest gap in known Plecoptera distribution); Gaufin et al. 1966, (key to adults, illustrations of male, female genitalia); Baumann, 1973, (description of nymph, SEM photos of mandibles); Baumann et al. 1977 (keys to nymphs, adults, illustrations of male, female genitalia); Stewart and Stark, 2002 (description and illustrations of nymph, probably *I. colubrinus*).

Male. — Brachypterous, forewing reaching Th_3, hindwing reaching Ab_2. Length of forewings 3.1–3.9 mm; length of body 16–20 mm. General body color brown to dark brown. Dorsum of head variable, with or without small light area along mesoanterior margin (Fig. 152); anterolateral irregular-shaped light areas variable, when present, large, between anterior-most portions of M-pattern and anterolateral margins of frons; large yellow, approximately triangular area with base along posterior margin of head,

extending mesoanteriorly to intersection of epicranial sutures; tiny dark brown setae absent. M-pattern variable, raised, without setae, usually medium brown throughout most of pattern, fading to light brown or yellow at anterior most portions, these blending in pigmentation with light anterolateral areas on frons, sometimes M-pattern all brown or mostly yellow, extending anteriorly to labrum, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas (Fig. 152). Interocellar area variable, generally light brown to brown with two, narrow, dark brown, transverse bands entering laterally, sometimes with narrow, light brown, median stripe, dark brown transverse bands entering area variable in height, arise from nearly black pigment enclosing large, lateral, medium brown rugosities; dark brown, narrow, longitudinal bands extend anteriorly to posterior margins of M-pattern; brown, dark brown and almost black areas variable, loosely form an H-shaped dark area (Fig. 152). Antennae variable, dark brown to yellow, with 52+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae. Pronotum with anterior and posterior transverse furrows deep, filled with dark brown, almost black along anterior border of anterior furrow and posterior border of posterior furrow; background pigmentation light brown, anterior and posterior margins brown to light brown; clothing setae short, densely scattered with small yellow spots at attachment points. Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, stripe width variable, generally widest posteriorly, tapering slightly anteriorly to posterior border of anterior transverse furrow, some specimens with stripe narrowly constricted at this point, expanding laterally above anterior furrow to anterior margin (Fig. 152). Mesonotum dark brown with variable and irregular areas of light pigment centrally and

along sutures of notal plates. Legs light brown to yellow, dark brown transverse band covering above and below femur-tibia joints, thin yellow pigment area at femur-tibia joints, outside, lateral femur with dense, clear, short, thin, clothing setae, dark brown and clear, short, erect setae scattered; with 1–2 variable length, thin hairless streaks on outer surface; tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along inside lateral and posterior margins. Abdomen light brown to brown with thick dark brown to black transverse bands along anterior margins of segments 2–9; first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown; dorsum entirely covered with dense, short, clear clothing setae, slightly longer on segments 3–9, along posterior margins; dorsolateral humps on terga 6–9 moderate, evident in dorsal view, posterior margins of terga 7–8 slightly swollen, those on eight largest, with dense patches of slightly longer, clear to golden clothing setae (Fig. 146, 148). Sternal lobe unusual, posteriorly not well defined, located slightly above mesoposterior margin of 7th sternite; mesoposterior margin of nail ending before reaching abdominal segment margin; mesoposterior abdominal segment margin rounded, produced slightly below posterolateral margins, similar mesoposterior marginal protrusions sometimes present on sterna six and eight; in other specimens, protrusions vestigial, without indication of nail other than slight rounded, mesoposterior protrusion of anterior dark pigment band. Hemitergal lobes in dorsal view of with lobe apices directed medially and slightly posteriorly, apical margins narrowly rounded, connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 146); 20–38 golden, mostly short, stout spinulae (sensilla basiconica) concentrated

along anterior distal sclerite margin and membranous tissue near sclerite (Figs. 146, 148); short, dark, erect setae interspersed with mostly short golden, fine setae, or all golden, fine setae scattered over entire posterior portion of lobe, usually continuing anteriorly, covering most of anterior membranous area. Epiproct apex modified in lateral view, mostly membranous, without sclerotized hook (Figs. 147, 159, 160); posterior margin without pair of ventrally or posteriorly directed hooks; in lateral view, under high magnification, anterior portion of epiproct with long, triangular, sharply pointed, scale-like setae, lateral margins without deep serrations (Fig. 161); anterior support sclerite trifid in anterior view, lateral arms longer and median arm shorter than base (Fig. 150), lateral arms in lateral view with apices curved smoothly to contour of anterior margin (Figs. 147, 159), median arm wide at base, tapering gradually to pointed apex, ending after surpassing 1/2 length of entire epiproct (Fig. 150); posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins mostly parallel to about mid-length, tapering gradually to narrow tip at apex (Fig. 149). Internal basal anchor in anterior view, with wide base tapering to where anterior keel-like sclerite connects, expanding gradually into large, broadly pointed lateral plates (Fig. 151); large, wing-like triangular sclerites dorsal-most, broadly curved, directed posterolaterally from centrally located narrow notch. Lateral stylets in lateral view with long, narrow base (Fig. 147); expanded areas at approximately 3/4 length of total epiproct from base; apical 1/4 wide, irregular-shaped at expanded region, margins tapering to broadly rounded tips; in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 149, 162); apical portions smoothly curved, apices directed dorsally. Paragenital plates large,

situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens. Subanal lobes rounded with dorsally and posteriorly directed lobe not completely sclerotized outside, membranous inside, lightly sclerotized plate light brown, its variable dorsal margin broadly to narrowly pointed, ending before membranous round margin; long, fine hair-like setae on posterior dorsal portion, becoming shorter on ventral portion. Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Fig. 154, 155); tiny, clear, erect setae densely scattered over entire surface of lateral lobes, few scattered near mesal apex; two small lobes dorsally, close to dorsoposterior, raised margin, may not be fully everted, their inverted bases only visible (Fig. 154); two small lobes ventrally, between lateral lobes, may not be fully everted, their bases only visible (Fig. 155); one large, mesally projected, rounded lobe, located apically as seen in dorsal or ventral views. Cercal segments light brown to brown, 30–32 segments, basal-most mostly sclerotized; basal 10–15 segments with slightly longer, golden, hair-like setae scattered, mostly at apical margins, these segments covered with short, dense, partially erect, golden setae; tiny, dark, erect, setae scattered on basal segments, less so, distally; groups of 3–6 long, golden, stout setae project ventrally from mesoposterior apical margins; distal segments with less dense, slightly shorter, clear, clothing setae.

Female. — Macropterous. Length of forewings 20–22 mm; length of body 17–25 mm. General body color, and head-pronotal pigmentation patterns somewhat similar to male; wingpads larger than male. Subgenital plate moderately broad at base, its width approximately 2/3 width of 8th sternum, a few sometimes wider; produced from 1/4 to

1/3 length of 9th sternum; posterior margin nearly quadrate or truncate with variable mesoposterior characters (Figs. 153, 163): 1. mesoposterior margin of subgenital plate with small to moderate, rounded, protruding nipple-like knob, 2. mesoposterior margin of subgenital plate with small to moderate, emarginated, protruding double nipple-like knob, 3. mesoposterior margin of subgenital plate nearly entire with vestigial emarginated double-protrusions barely visible; dark pigmentation variable, usually along posterior margin, sometimes restricted to mesoposterior margin, laterally with two, small, brown markings on plate, below mesally angled posterior margins of abdomen, and variable pair of thin to wide longitudinal dark bands anteriorly on segment.

Nymph. — General body color brown to light brown with light and dark markings (Fig. 145). Antennae golden to light brown; with short, erect, stout, golden peg-like setae arranged as apical whorls on segments 1–2, a few scattered on dorsal surface of segment one, remaining segments with smaller, erect, golden peg-like setae in apical whorls; usually with long sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 15–22; long, golden, intersegmental clothing setae on segment 1–2, with several scattered, short, fine, clear, erect setae. Dorsum of head with contrasting pigment pattern; fine short, golden, clothing setae sparsely scattered; light colored narrow band forming M-pattern between antennal bases and median ocellus usually open mesoanteriorly; anterior transverse brown band thick laterally, faded, mostly open mesally, incompletely enclosing M-pattern anteriorly; anterior margin with narrow transverse light band, generally extending mesoposteriorly to median ocellus, brown areas below variable, usually with two wide, transversely flattened light areas above anterior-most portions of M-pattern, sometimes open anteriorly; two small,

irregular-shaped dark markings on anterolateral margins between antennal bases and labrum; labrum with two, small, semicircular dark markings along anterior margin; variable, flatly rounded, curved, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern; variable, usually small, triangular-shaped light areas along outer lateral margins of lateral ocelli; recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows with sparsely scattered, short, thin, erect setae interspersed, extending posteriorly from below epicranial arm sutures to inner occipital spinule rows. Interocular area variable, usually brown, similar to adjacent areas anteriorly, posteriorly with variable mesoposterior faded area, sometimes extending posteriorly to epicranial suture intersection; post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction, sometimes interrupted. Lacinia with 1 axilary seta, 18–24 marginal setae below subapical tooth, 11–17 submarginal setae, scattered from below apical tooth downwards to base. Left and right mandible under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually extending beyond 1/2 length of cusp (Fig. 10) (Baumann 1973). Submental gills at least 2x as long as width at base. Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs; anterior and posterior transverse furrows filled with medium to dark brown, anterior and posterior margins usually with similar pigment, lateral margins light; central pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of partially light colored dorsal suture, extending posteriorly to almost entire length of discs, these bands join mesally for most

their length; dark and light brown bands radiate from mesoanterior to posterolateral areas, usually enclosed by light tan or light brown, these brown bands bordered by variable areas of light, rounded areas, remainder of pronotum mostly brown; anterior and lateral margins with continuous, short, stout, peg-like setae; posterior margin with peg-like setae mixed with longer, golden, stout, erect setae; pronotum covered with moderately dense, short, clear, clothing setae. Meso-Metanota partially brown, usually mesoanterior light oval areas filled partially with light brown or tan, anterior and inner lateral, thin, dark pigment borders with short, stout setae, sometimes faded in alcohol; long, thin, curved, posteriorly widened, light areas sometimes with lateral dark margins poorly defined in preserved material; variable hour glass-shaped light area along mesoposterior margins, usually smaller on metanotum. Abdominal terga usually with indistinct, thin, mesally interrupted, anterior and posterior dark transverse bands on segments 1–9, segment 1 anterior bands variably shaped, segment 10 with anterior band only and mesoposteriorly produced, these bands often faded in preserved material; short, clear to golden, clothing setae interspersed between stout spines; posterior margins with continuous row of spinules, those on 10th tergum sometimes in multiple rows along mesoposterior margin, Posterior setal row of male 8th abdominal sternum usually not interrupted mesally in mature nymphs, slightly interrupted in immature. Cercal segments golden; apical whorl of short, stout setae, those located at mesoposterior apical margin, similar in length to rest of whorl.

Ovum. — General shape oval, triangular cross section (Fig. 156). Color brown. Length 448.9–497.6 µm, width 312.2–341.5 µm. Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, with three large stabilizing carinulae

at each anterior angle (Fig. 157). Chorionic surface granular (Fig. 158). Hexagonal follicle cell impressions absent. Micropyle row subequatorial; orifices located within unevenly raised, slightly carinate, apical portions of micropylar tubes (Fig. 158). Occasionally orifices with upright, plate-like sperm guides.

Material examined**.** — TYPES: *I. zionensis*, Holotype ♂, UTAH: Washington Co., Zion National Pk., River ?, 21/VI/1942, C.P. Alexander (NMNH). Paratypes; *I. zionensis*, UTAH: Washington Co., Zion National Pk., River ?, 22/VI/1942, C. Alexander, 1 ♂ (NMNH), Zion National Pk. in spider web, River ?, 22/VI/1942, C. Alexander, 1 ♂ (NMNH).

Additional specimens — *CAN*: BRITISH COLUMBIA: “291”, Sikanni R., 18/VI/1958, C. Lindroth, 1 ♂, 1 ♀ (NMNH).

NORTHWEST TERRITORIES: Mouth of Keele River, Mackenzie R., 26/VI/1953, P.M. Mann, 2 ♂, 2 ♀ (BYU).

USA: ARIZONA: Apache Co., Wagon Wheel Campground, Lukachukai Cr., 18/V/1970, R.W. Baumann, 5 Nymphs (BYU), Mouth, Chusika Mts., Lukachukai Cr., 2/VI/1982, R.W. Baumann & Clark, 5 ♂ (BYU), Wagon Wheel Campground, Lukachukai Cr., 2/VI/1982, R.W. Baumann, Clark & Mower, 6 ♂ (BYU), Wagon Wheel Campground, Lukachukai Cr., 2/VI/1982, R.W. Baumann, Clark & Mower, 7 ♂ (BYU), Wagon Wheel Campground, Lukachukai Cr., 2/VI/1982, R.W. Baumann, Clark & Mower, 2 ♀ (BYU).

COLORADO: Chaffee Co., T12S, R79W, S35 at Riverside Bridge, Arkansas R., 11/VI/1985, S. Herman, 2 ♂ (CSU), Riverside Bridge, Arkansas R., 11/VI/1985, S. Herrman, 1 ♂ (BYU); Conejos Co., Location ?, Rio Conejos, 17/VI/1986, R.L. Hassage, 5 ♂ (reared), 6 ♀ (reared) (UNT); Gunnison Co., junction of Soap Cr., Gunnison R.,

15/VI/1962, A.W. Knight, 6 ♂, 2 ♀ (BYU), junction of Soap Cr., Gunnison R., 20/IV/1962, A.W. Knight, 1 Nymph (BYU), junction of Soap Cr., Gunnison R., 7/VI/1961, A.W. Knight, 1 Nymph (BYU), 2 mi. below Hwy 149, Lake Fork Gunnison R., 16/VI/1962, A.W. Knight, 6 ♂ (BYU); San Miguel Co., Confluence with Specie Cr. M44 Rd., San Miguel R., June-July 1999, J.B. Sandberg, 12 ♂ (reared), 15 ♀ (reared), 2 Nymphs (JBS), Placerville bridge, San Miguel R., June-July 1999, J.B. Sandberg, 45 ♂ (reared), 41 ♀ (reared) (JBS), Placerville bridge, San Miguel R., 20/VI/1999, J.B. Sandberg, 10 ♂ (reared) (JBS), Placerville bridge, San Miguel R., 19/IV/1986, K.W. Stewart, 6 ♂ (reared), 18 ♀ (reared) (UNT), Placerville bridge, San Miguel R., 19/V/1986, K.W. Stewart & R.L. Hassage, 6 ♂ (reared), 1 ♀ (reared) 17 Nymphs (UNT), Placerville bridge, San Miguel R., 24/V/1981, K.W. Stewart & B.P. Stark, 2 ♂ (reared), 1 ♀ (UNT), Roadside Camp 4 mi. N. of Placerville Hwy 64, Leopard Cr., 28/V/1999, J.B. Sandberg, 1 ♀ (reared) (JBS), Roadside Camp 4 mi. N. of Placerville Hwy 64, Leopard Cr., 15/VIII/1999, J.B. Sandberg, 5 Nymphs (JBS), Roadside Camp 4 mi. N. of Placerville Hwy 64, Leopard Cr., 14/III/2000, J.B. Sandberg, 2 Nymphs (JBS), Roadside Camp 4 mi. N. of Placerville Hwy 64, Leopard Cr., 30/VI/2000, J.B. Sandberg, 3 ♂ (reared), 5 ♀ (reared), 5 Nymphs (JBS); Summit Co., State Wildlife Area Hwy 9, 11 mi. N of Silverthorn, Blue R., 22/III/1997, J.B. Sandberg, 24 Nymphs (JBS), State Wildlife Area Hwy 9, 11 mi. N of Silverthorn, Blue R., June1997, J.B. Sandberg, 13 ♂ (reared), 58 ♀ (reared), 16 Nymphs (JBS), State Wildlife Area Hwy 9, 11 mi. N of Silverthorn, Blue R., 1/IVI/1999, J.B. Sandberg, 45 Nymphs (JBS).

NEW MEXICO: Rio Arriba Co., Chama, Rio Chama, 19/IV/1973, T. Wolf, 1 ♂, 2 Nymphs, 1 exuviae (BPS), Chama, Rio Chama, 8/VI/1974, T. Wolf, 10 Nymphs (BPS),

Chama, Rio Chama, 8/VI/1974, B. Stark & T. Wolf, 1 ♂, 2 ♀, 1 Nymph (BYU), 1 mi. N. of Chama, Hwy 17, Rio Chama, 23/V/1998, C.R. Nelson, B.P. Stark & I. Sivec, 5 Nymphs (BYU); Lincoln Co., Bonito Lake, 10 mi. N. of Ruidoso, Rio Bonito, 11/III/1967, M. Franko, 1 Nymph (BYU); Taos Co., 3 mi. E. of Cuesta, Red ?, 9/VI/1974, B.P. Stark & T. Wolf, 3 Nymphs (BYU).

UTAH: Carbon Co., junction Nine Mile Creek, Minnie Maud Cr., 1/VI/1978, R.W. Baumann & Winget, 1 ♂ (BYU), Below grassy Trial Reservoir, Grassy Trial Cr., 5/V/1989, R.W. Baumann, 1 Nymph (BYU), Sunnyside, Grassy Trial Cr., 5/V/1989, R.W. Baumann, 2 ♂ (BYU), Price, Price R., 23/III/1970, R. Matekovic, 1 Nymph (BYU); Duchesne Co., Above Starvation Reservoir., Strawberry R., 26/V/1974, D. Alstad & G.F. Edmunds, 1 ♂ (reared) (BPS), Above Starvation Reservoir, Strawberry R., 26/V/1974, D. Alstad & G.F. Edmunds, 2 ♀ (reared) (BPS), Above Starvation Reservoir, Strawberry R., 23/V/1974, B.P. Stark & D. Alstad, 1 Nymph (BYU), Starvation Reservoir, Strawberry R., 4/V/1975, D. Alstad & M. Alstad, 12 Nymphs (BPS), Emery Co., Hwy 10 SW. of Emery, Quitchupah Cr., 18/V/2001, R.W. Baumann, 1 ♂, 1 ♀ (BYU); San Juan Co., Newspaper Rock State Pk. on Rt. 211, Indian Cr., 5/VI/1994, B.C. Kondratieff, 3 ♂, 5 ♀, 1 Nymph (CSU); Sevier Co., I-70, Exit 72, E. of Salina, Salina Cr., 13/V/1998, C.R. Nelson, B.P. Stark & I. Sivec, 5 Nymphs (BYU); Utah Co., Junction Little Diamond Creek, Diamond Fork Cr., 14/IV/1987, C.R. Nelson & Wells, 3 Nymphs (BYU), Junction Diamond Fork Creek, Little Diamond Cr., 23/V/1987, C.R. Nelson & J.R Nelson 2 ♂ (BYU); Washington Co., Zion National Pk., Virgin R., 20/III/1960, A.R. Gaufin, 4 Nymphs (NMNH), North Fork Virgin-Mile 11.7, Zion National Pk., Big Bend R., 18/I/1996, M. Shakarjian, 2 Nymphs (UNT), North Fork Virgin-Mile 11.7, Zion National

Pk., Big Bend R., 13/II/1996, M. Shakarjian, 2 Nymphs (UNT), North Fork Virgin-Mile 11.7, Zion National Pk., Big Bend R., 10/IV/1996, M. Shakarjian, 2 Nymphs (UNT).

Distribution. — CANADA: British Columbia, Northwest Territories; USA: Alaska (Stark et al. 1986), Arizona, Colorado, New Mexico, Utah (Fig.2).

Diagnosis and Discussion. — The membranous male epiproct distinguishes this species from all the *Isogenoides* (Fig. 147). Females are most similar to *I. elongatus* and can tentatively be separated from them by their slightly narrower subgenital plate and sometimes-larger mesoposterior protrusion (Fig. 153). Due to these characters occasional overlap, separation of females may require males to be collected simultaneously in areas of overlapping distribution. Nymphs are inseparable from *I. elongatus*, except when live, or recently preserved. Those of *I. elongatus* (Fig. 50) may be darker brown when compared to the light brown, almost yellow background pigment of *I. zionensis* (Fig. 145).

Some life history details for this species were reported for a large population in Southern Colorado (DeWalt & Stewart 1995). They determined a semivoltine lifecycle with observed delay in egg development over the first summer and winter, at least for some eggs. Shakarjian (1997) suggested that *I. zionensis* had a univoltine life cycle and no egg diapause in the North Fork Virgin River, Zion Nation Park, Utah.

Specimens available indicate that emergence begins in late May and continues until early July, with peak emergence in occurring in late June.

Discussion

Eight species of *Isogenoides* are now known with species keys provided for all life stages, diagnoses based on male and female external genitalia, internal male

genitalia, and ova using light and scanning electron microscopy. *Isogenoides krumholzi* (Ricker) is now placed into with synonymy with *I. doratus* (Frison). This revision of the Nearctic *Isogenoides* contributes to the call for a more credible, holomorphological approach proposed by Hennig (1966, 1981), Ross (1974), Stewart (1997, 2001), and Wiggins (1981).

Relatively little is known about the biology of the species in *Isogenoides* except that of the adult drumming behavior (Maketon et al. 1988, Stewart and Zeigler 1984, Sandberg and Stewart 2003, Zeigler and Stewart 1977). Shakarjian (1997) determined that *I. zionensis* had a univoltine life cycle and that egg development was direct for a Virgin River, Utah population. Hilsenhoff and Billmyer (1973) and Dosdall and Lemkuhl (1979) reported univoltine life cycles for *I. frontalis* in Wisconsin and Saskatchewan respectively. DeWalt and Stewart (1995) reported a 9–10 month egg diapause and semivoltine life cycle for a Rio Conejos *I. zionensis* population. In the fall months of Wisconsin, Shapas and Hilsenhoff (1976) found the nymphal gut-contents of *I. frontalis* to be 50% by volume Chironomidae and other Diptera. Much remains to be discovered concerning the biology of these exciting stoneflies.

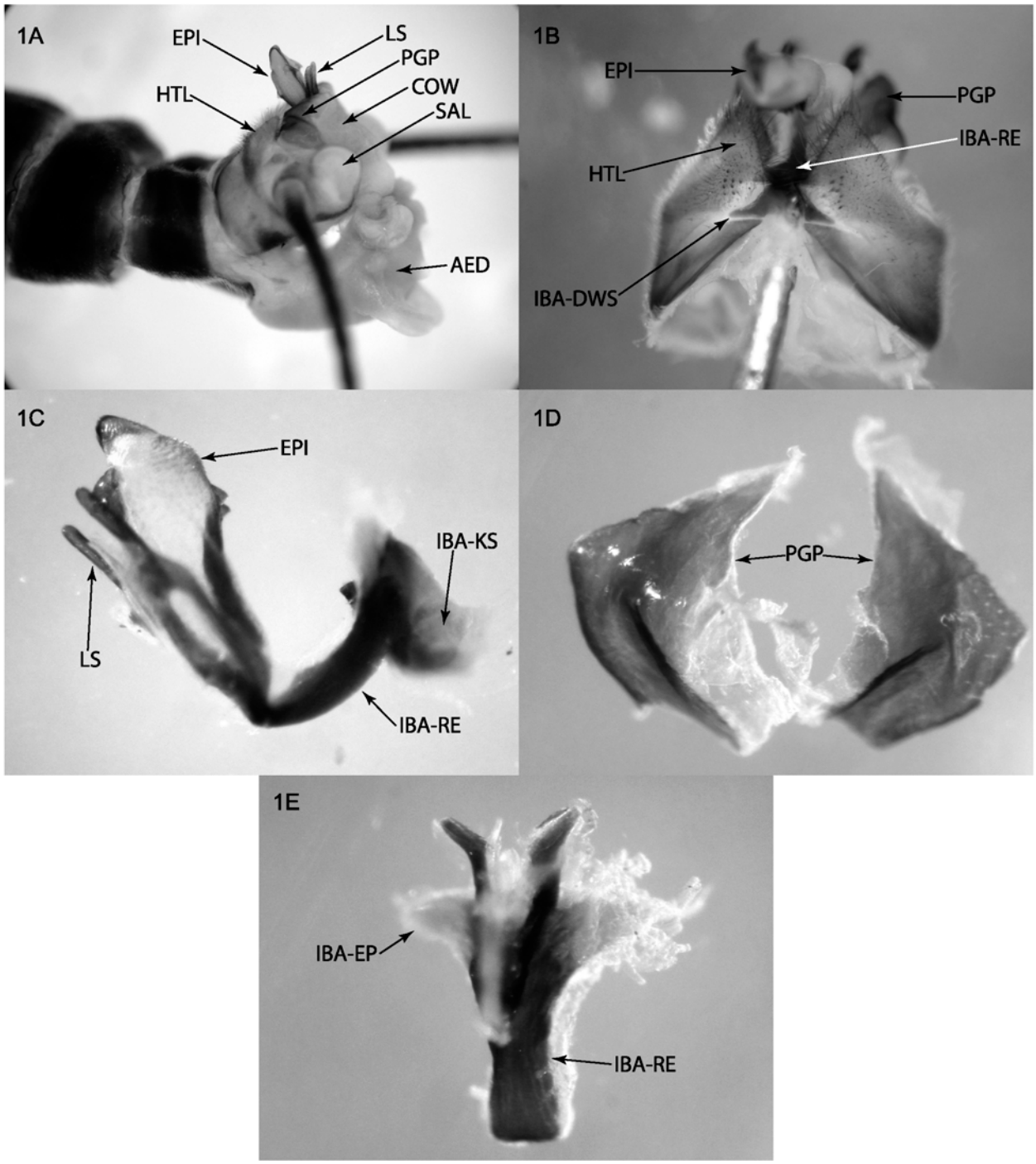


Figure 1. Digital photos of *Isogenoides varians* male internal and external genitalia. 1A. Lateral view of male Ab_{8-10} with everted aedeagus. 1B. Dorsal view of Ab_{10}. 1C. Lateral view of epiproct, lateral stylets and internal basal anchor. 1D. Paragenital plates dissected. 1E. Anterior view of basal internal anchor. (**A**=aedeagus, **C**=cowl, **DWS**=dorsal wing-like sclerites, **E**=epiproct, **EP**=expanded lateral plates, **HTL**=hemitergal lobes, **IBA**=internal basal anchor, **KS**= keel-like sclerite, **LS**=lateral stylets, **PGP**=paragenital plates), **RE**=rod-like extension. Character terminology after Stark and Nelson (2000).

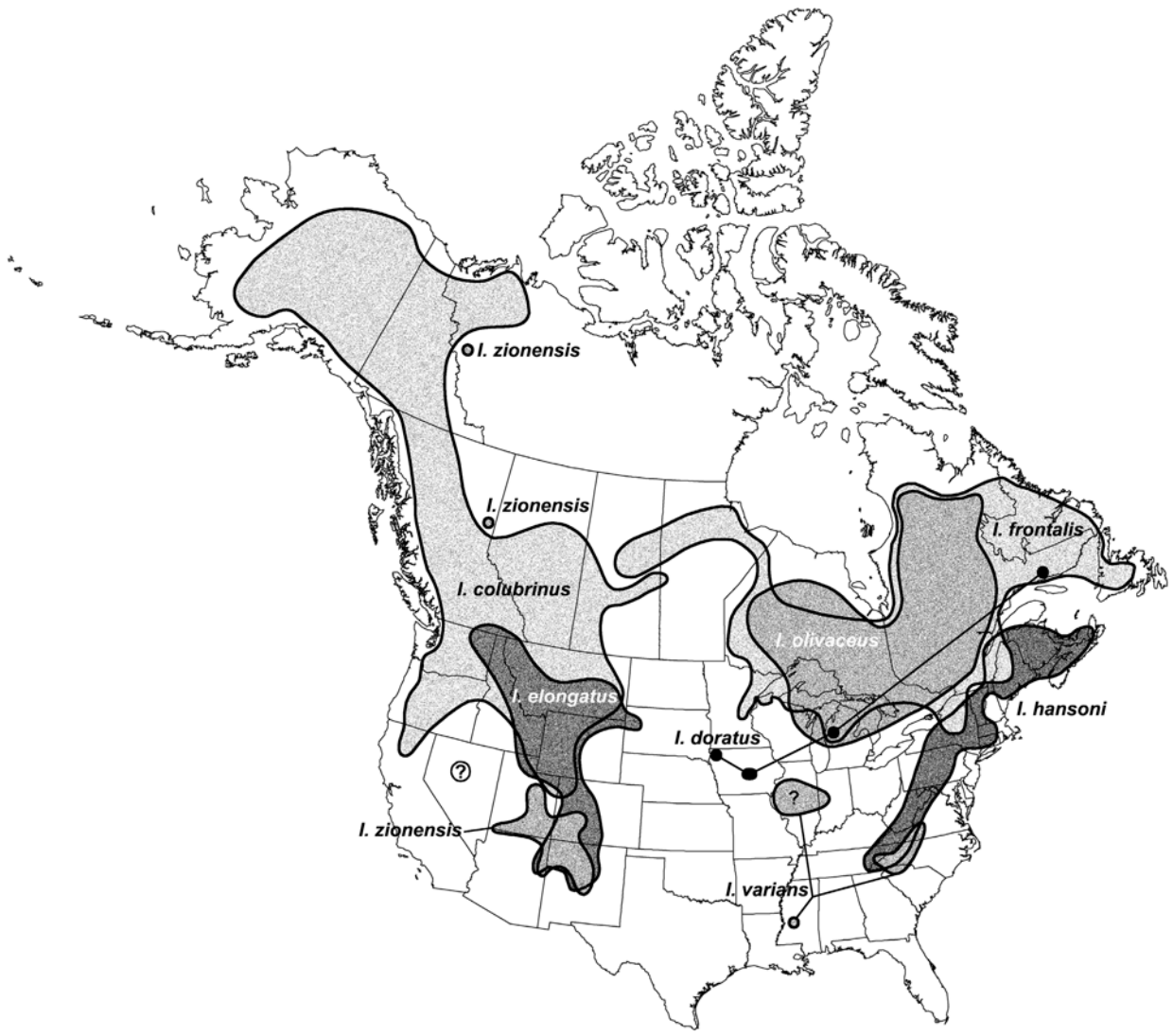
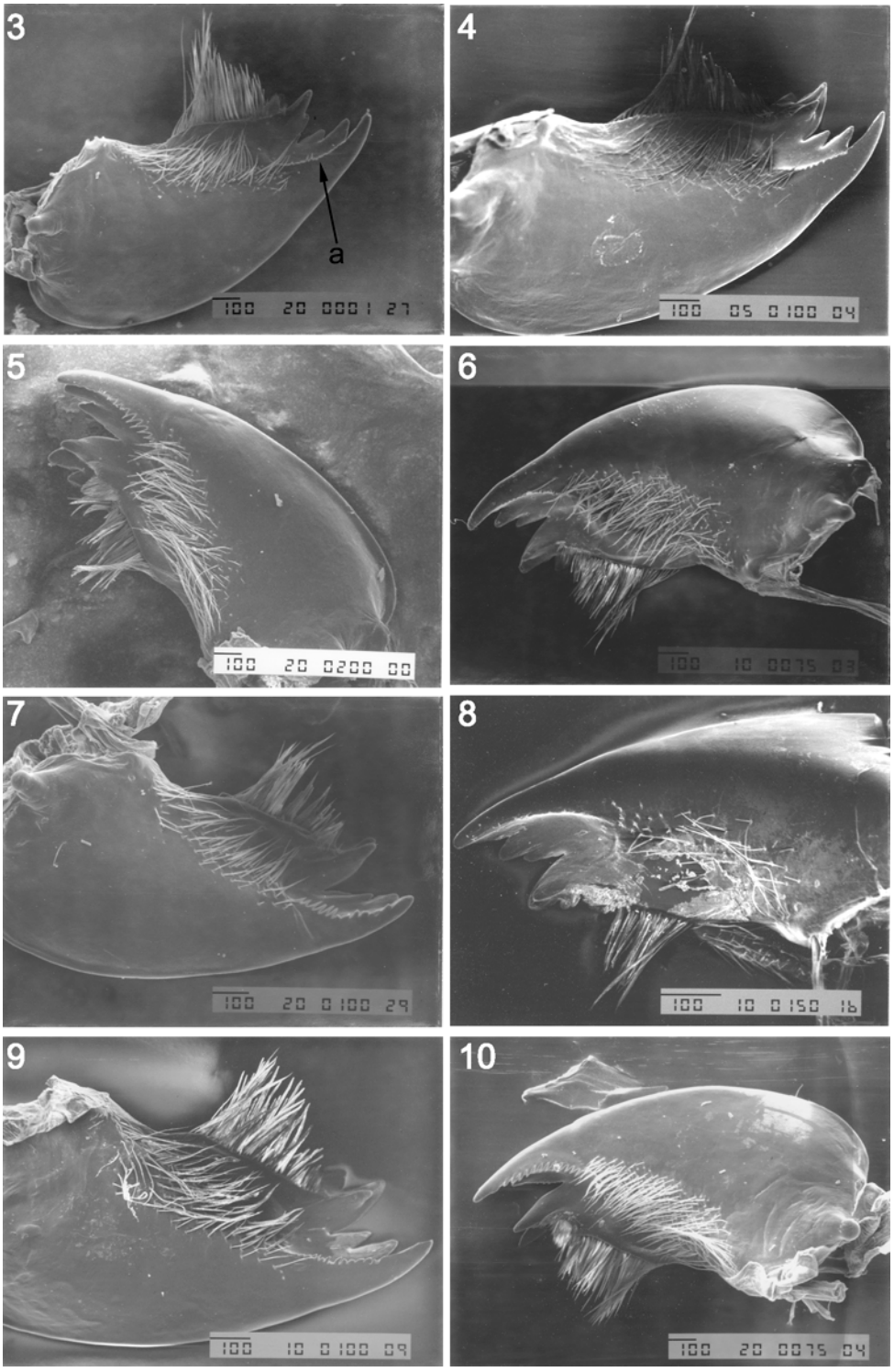


Figure 2. The geographic distribution of *Isogenoides* species. Shaded regions represent confirmed and probable locations only; published records without detailed location data are listed and cited within the Distribution-section under each species account.



Figures 3–10. Left nymphal mandible, ventral (75–100X): 3. *I. colubrinus*. a, distal-most cusp with inconspicuous serrations. 4. *I. doratus* distal-most cusp with inconspicuous serrations. 5. *I. elongatus* distal-most cusp with conspicuous serrations. 6. *I. frontalis* distal-most cusp with inconspicuous serrations. 7. *I. hansoni* distal-most cusp with conspicuous serrations. 8. *I. olivaceus* distal-most cusp with inconspicuous serrations. 9. *I. varians* distal-most cusp with conspicuous serrations. 10. *I. zionensis* distal-most cusp with conspicuous serrations. (SEM's by B.P. Stark).

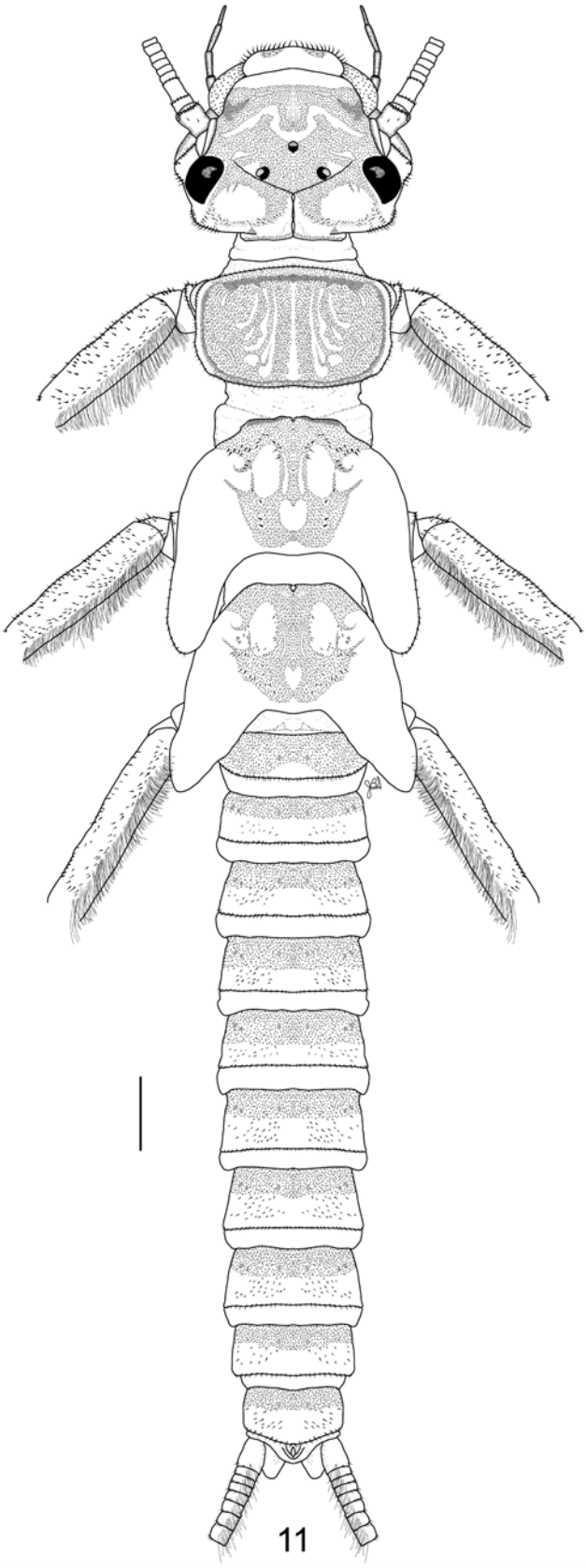
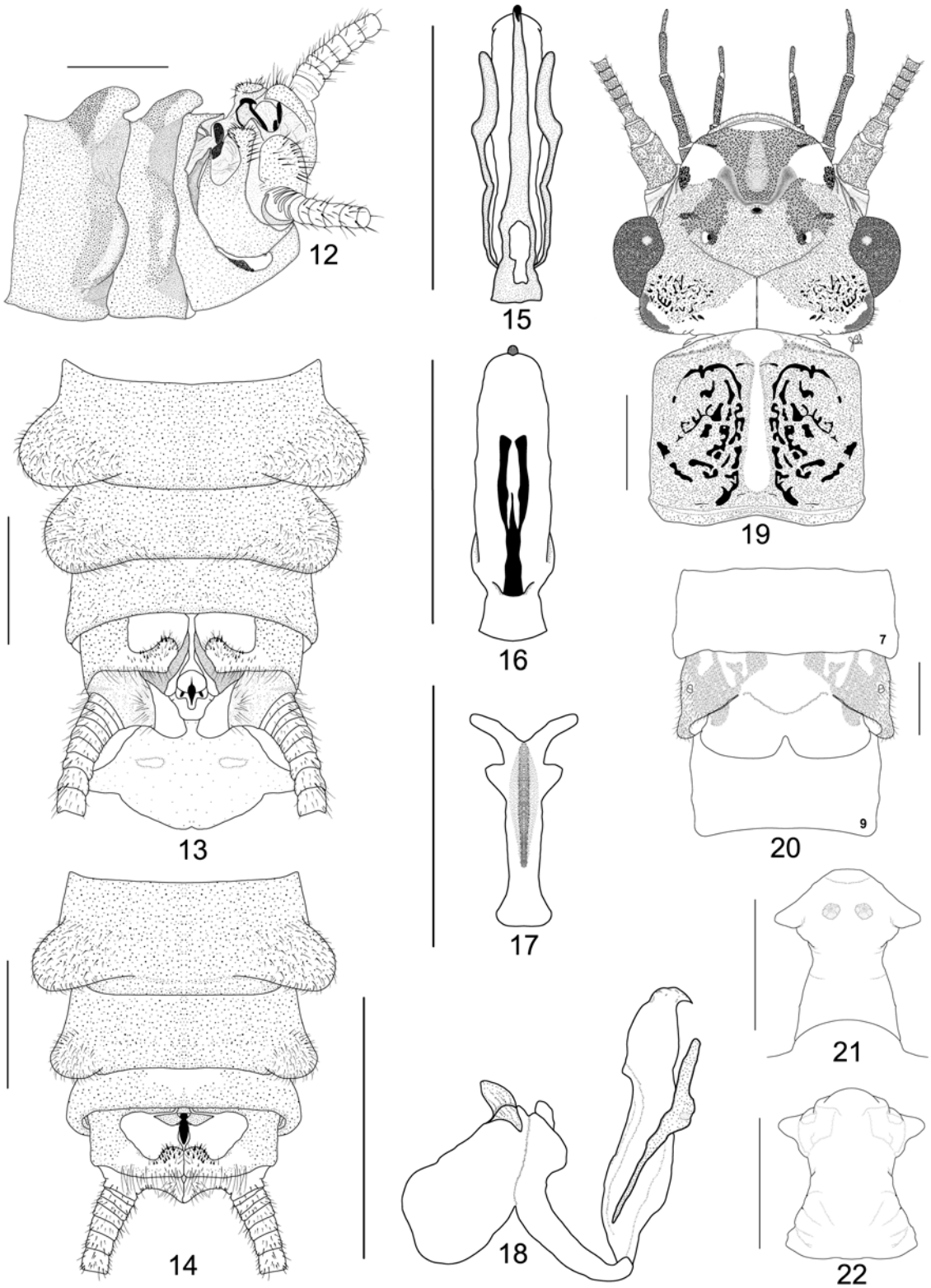
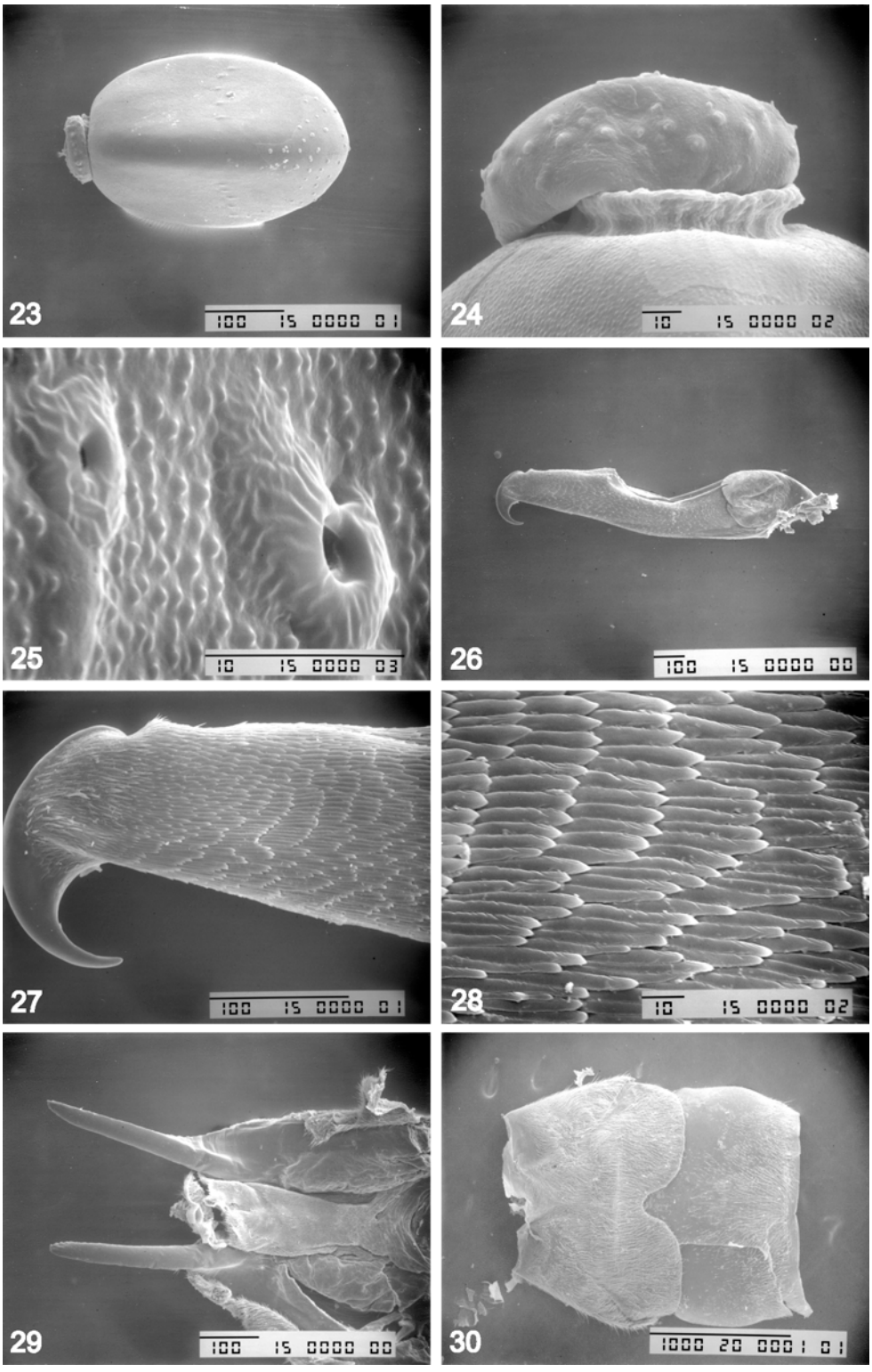


Figure 11. *Isogenoides colubrinus*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 12–22. *Isogenoides colubrinus*. 12. male abdomen, oblique-lateral, 25x. 13. male abdomen, everted, dorsal, 32x. 14. male abdomen, non-everted, dorsal, 32x. 15. epiproct and stylets, posterior, 50x. 16. epiproct, anterior, 50x. 17. internal basal anchor, anterior, 50x. 18. epiproct, stylet and internal basal anchor, lateral, 50x. 19. male head and pronotum 32x. 20. female subgenital plate, sternites 7–9, 25x. 21. aedeagus, dorsal, 50x. 22. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 23–30. *Isogenoides colubrinus*. 23. whole ova 200x. 24. detail of collar 1,000x. 25. detail of micropyles 5,000x. 26. epiproct, lateral view, 75x. 27. detail of apex 350x. 28. detail of scale-like setae 1,000x. 29. stylets, anterior view, 150x. 30. subgenital plate, segments 8-9, 35x.

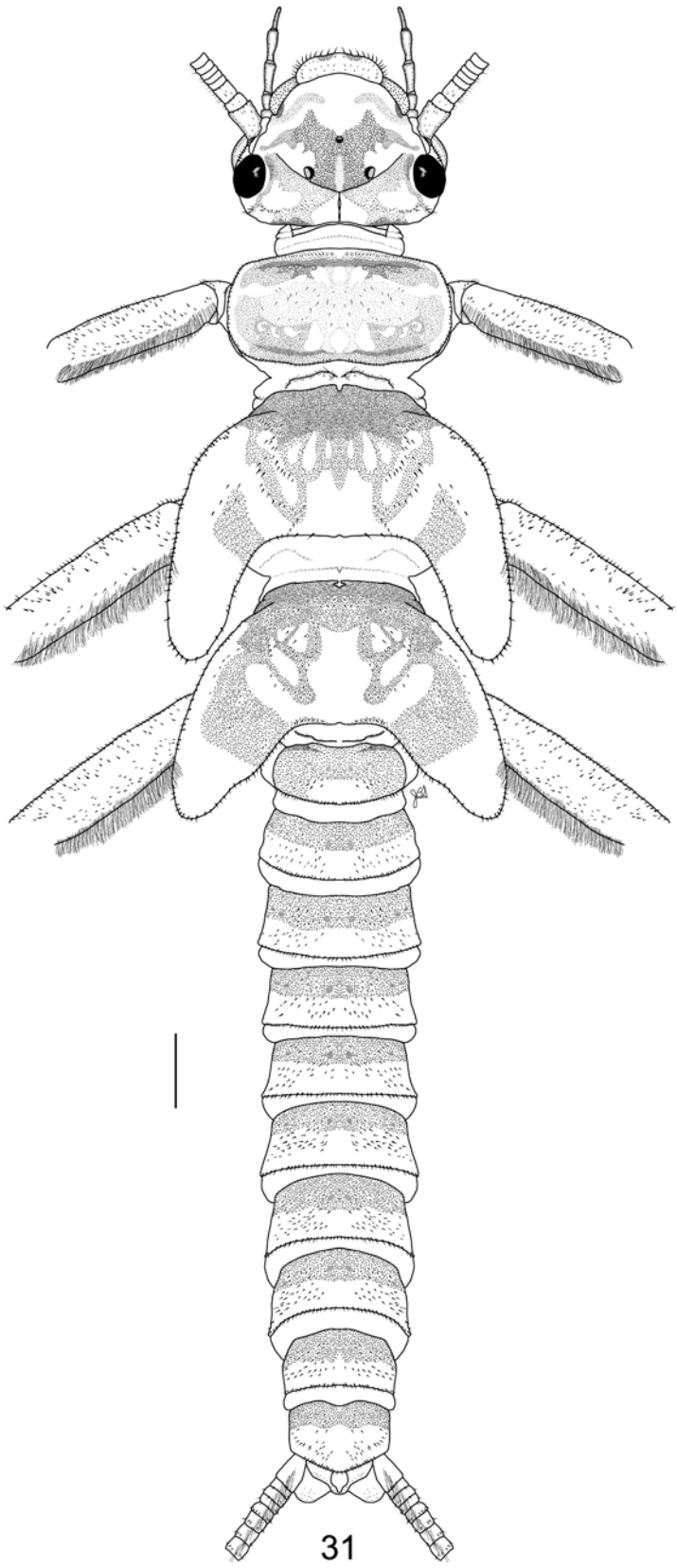
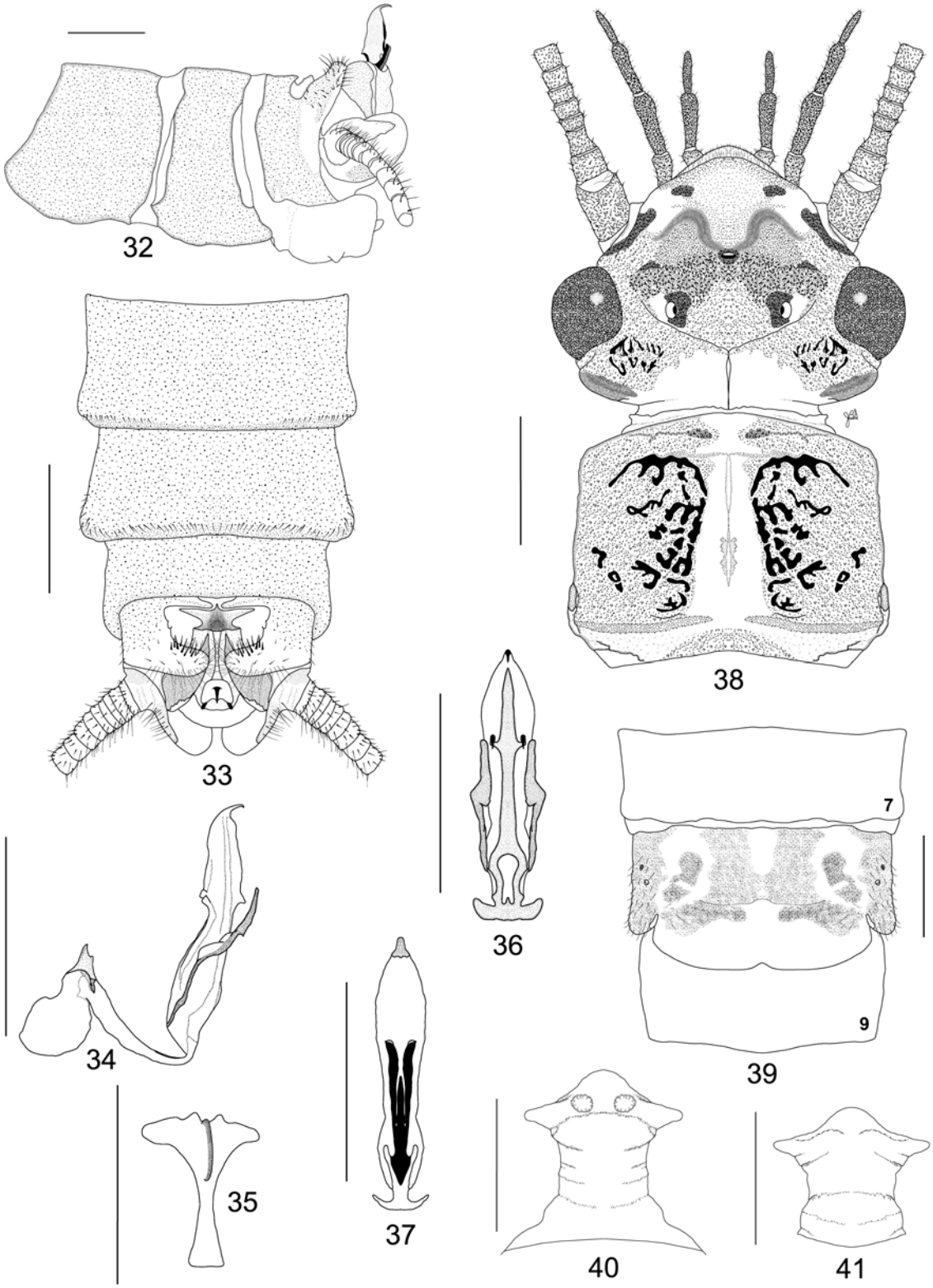
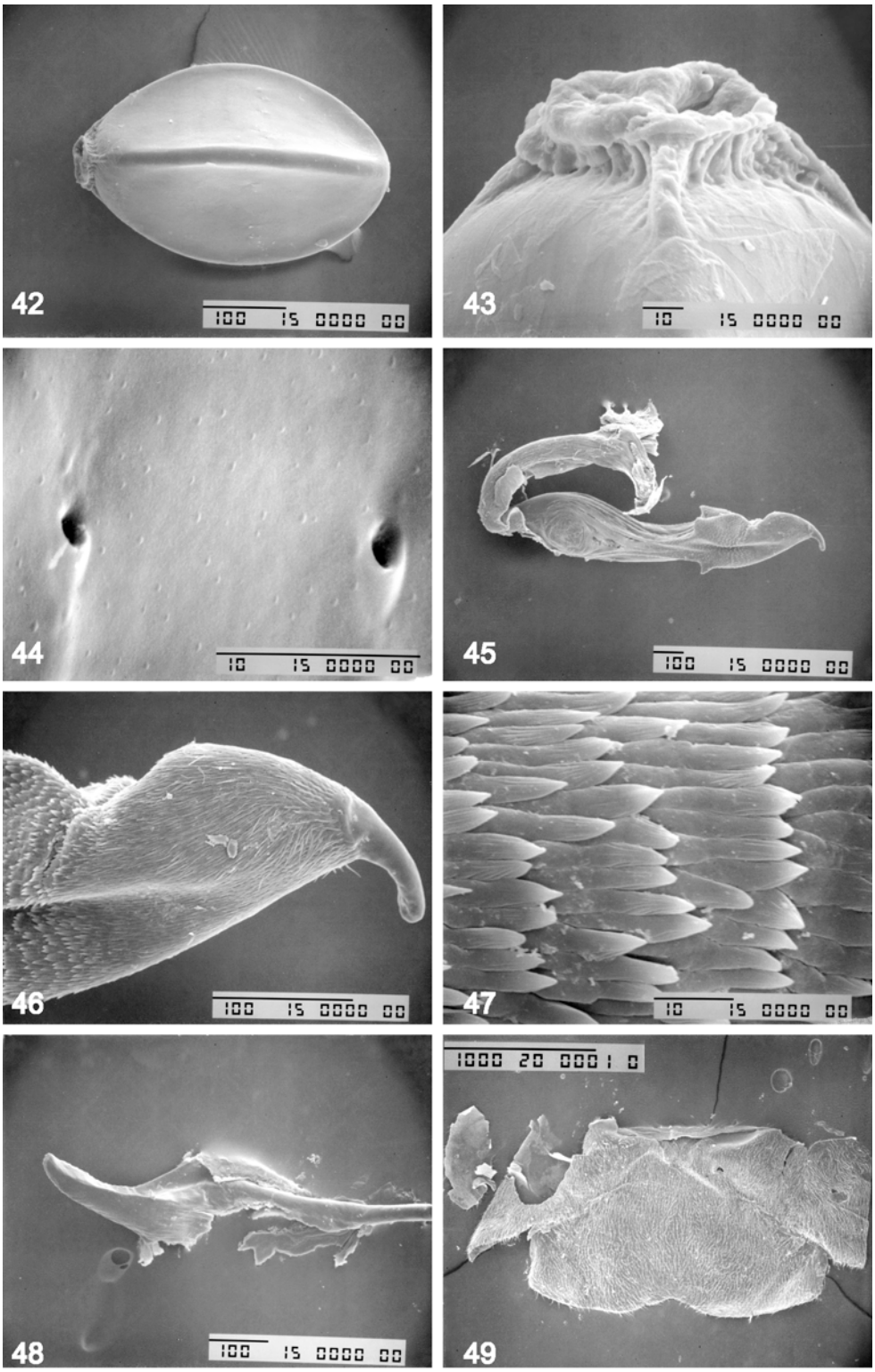


Figure 31. *Isogenoides doratus*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 32–41. *Isogenoides doratus*. 32. male abdomen, lateral, 25x. 33. male abdomen, non-everted, dorsal, 32x. 34. epiproct, stylet and internal basal anchor, lateral, 50x. 35. internal basal anchor, anterior, 50x. 36. epiproct and stylets, posterior, 50x. 37. epiproct, anterior, 50x. 38. male head and pronotum 32x. 39. female subgenital plate, sternites 7–9, 25x. 40. aedeagus, dorsal, 50x. 41. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 42–49. *Isogenoides doratus*. 42. whole ova 200x. 43. detail of collar 1,000x. 44. detail of micropyles 5,000x. 45. epiproct and internal basal anchor, lateral view, 75x. 46. detail of apex 350x. 47. detail of scale-like setae 2,000x. 48. right stylet, anterior view, 150x. 49. subgenital plate, segment 8, 35x.

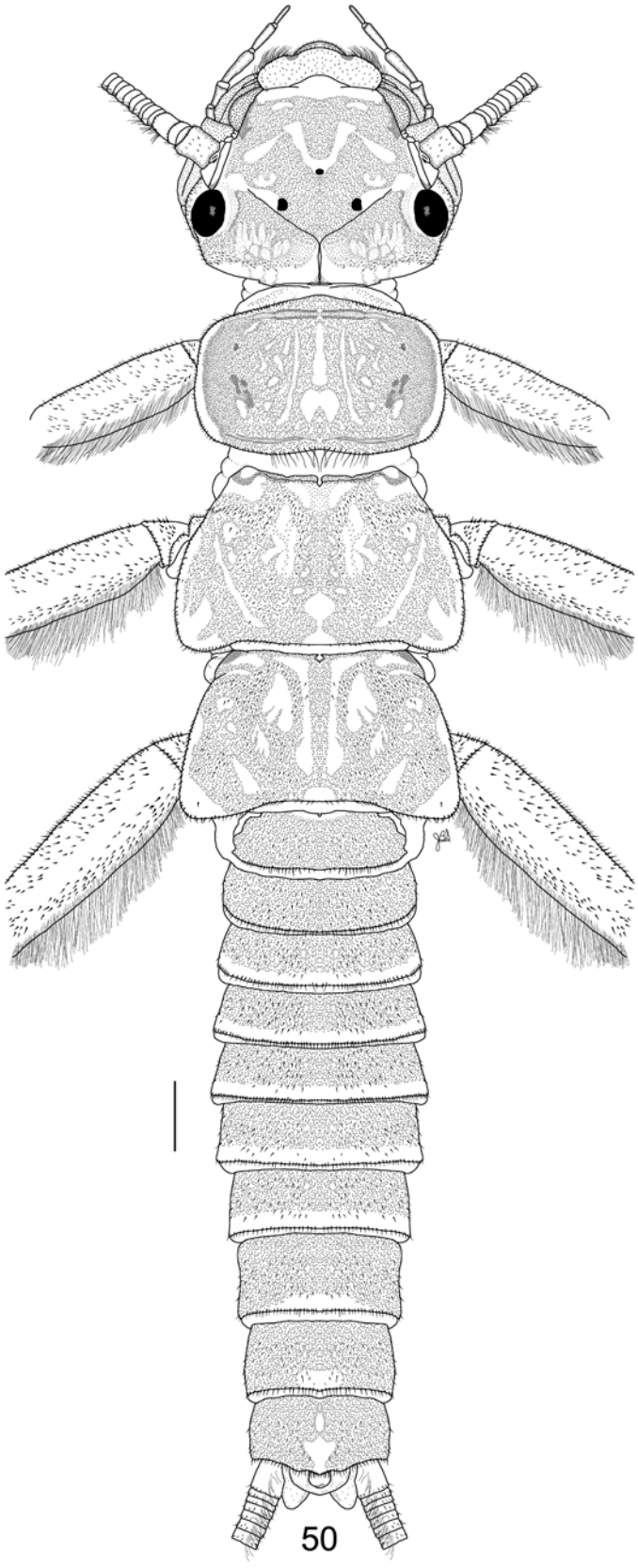
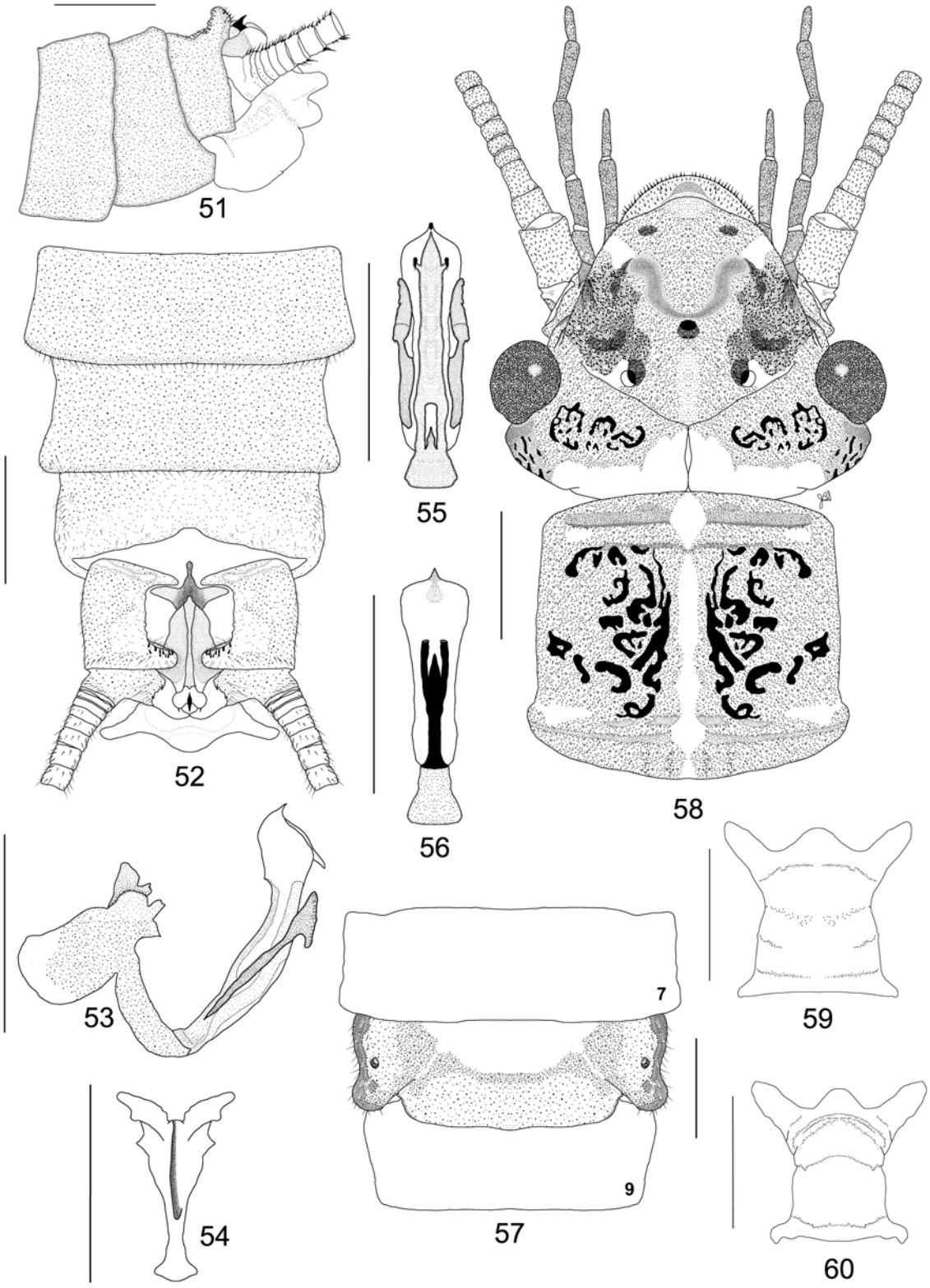
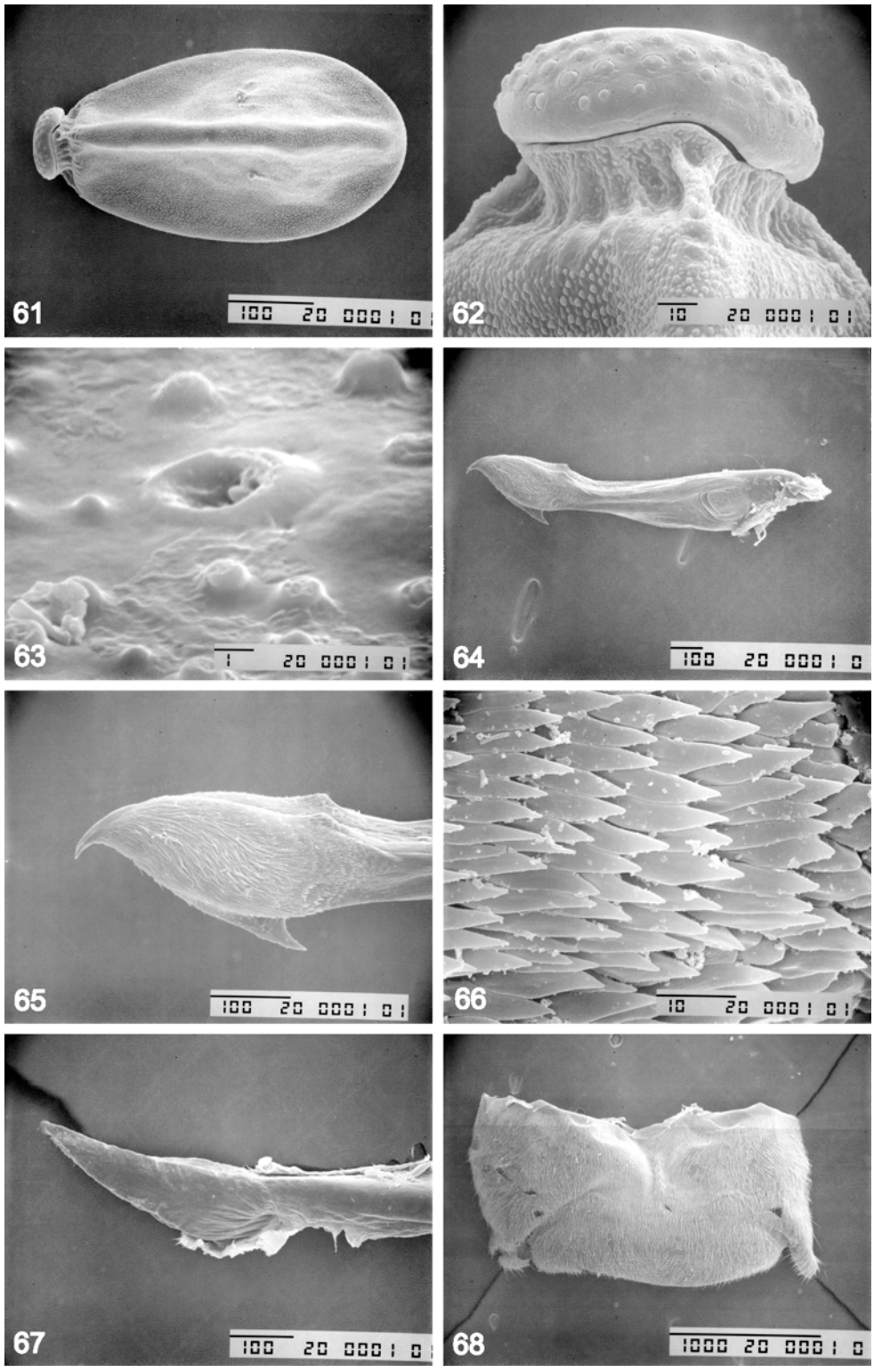


Figure 50. *Isogenoides elongatus*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 51–60. *Isogenoides elongatus*. 51. male abdomen, lateral, 25x. 52. male abdomen, everted, dorsal, 32x. 53. epiproct, stylet and internal basal anchor, lateral, 50x. 54. internal basal anchor, anterior, 50x. 55. epiproct and stylets, posterior, 50x. 56. epiproct, anterior, 50x. 57. female subgenital plate, sternites 7–9, 25x. 58. male head and pronotum 32x. 59. aedeagus, dorsal, 50x. 60. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 61–68. *Isogenoides elongatus*. 61. whole ova 200x. 62. detail of collar 1,000x. 63. detail of micropyles 10,000x. 64. epiproct, lateral view, 75x. 65. detail of apex 200x. 66. detail of scale-like setae 1,500x. 67. right stylet, anterior view, 200x. 68. subgenital plate, segment 8, 35x.

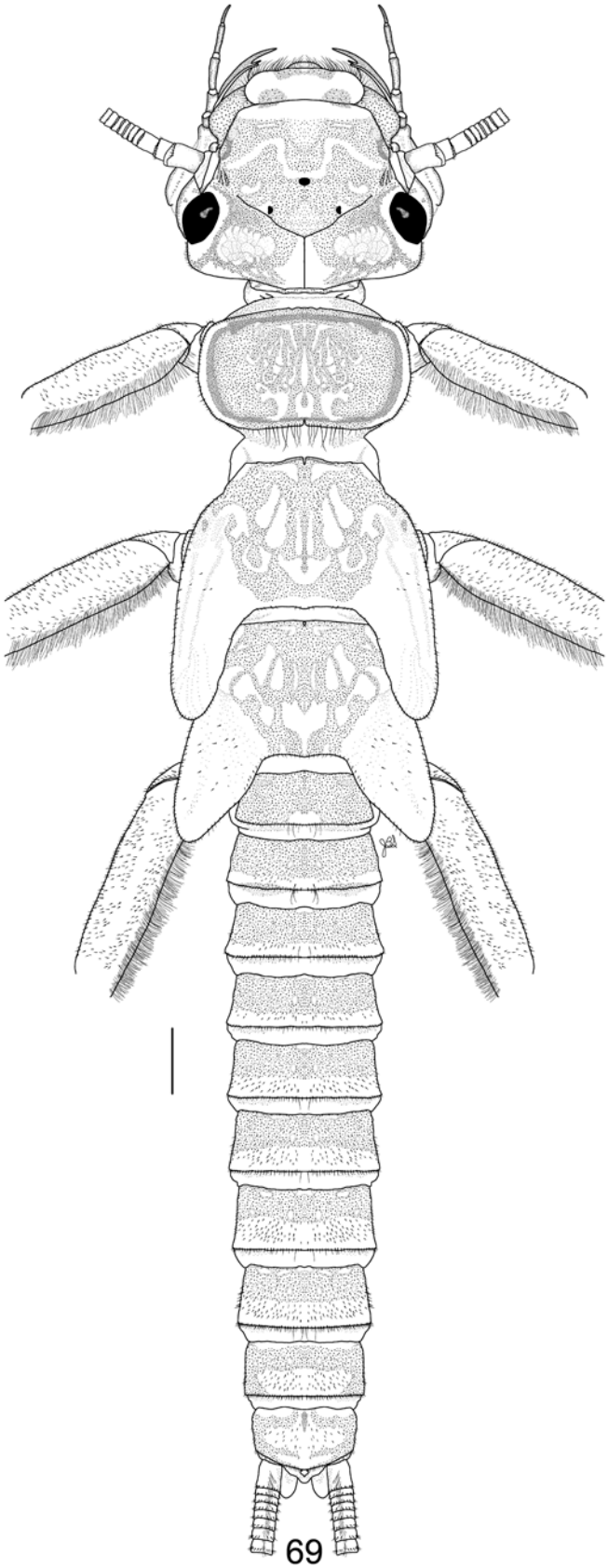
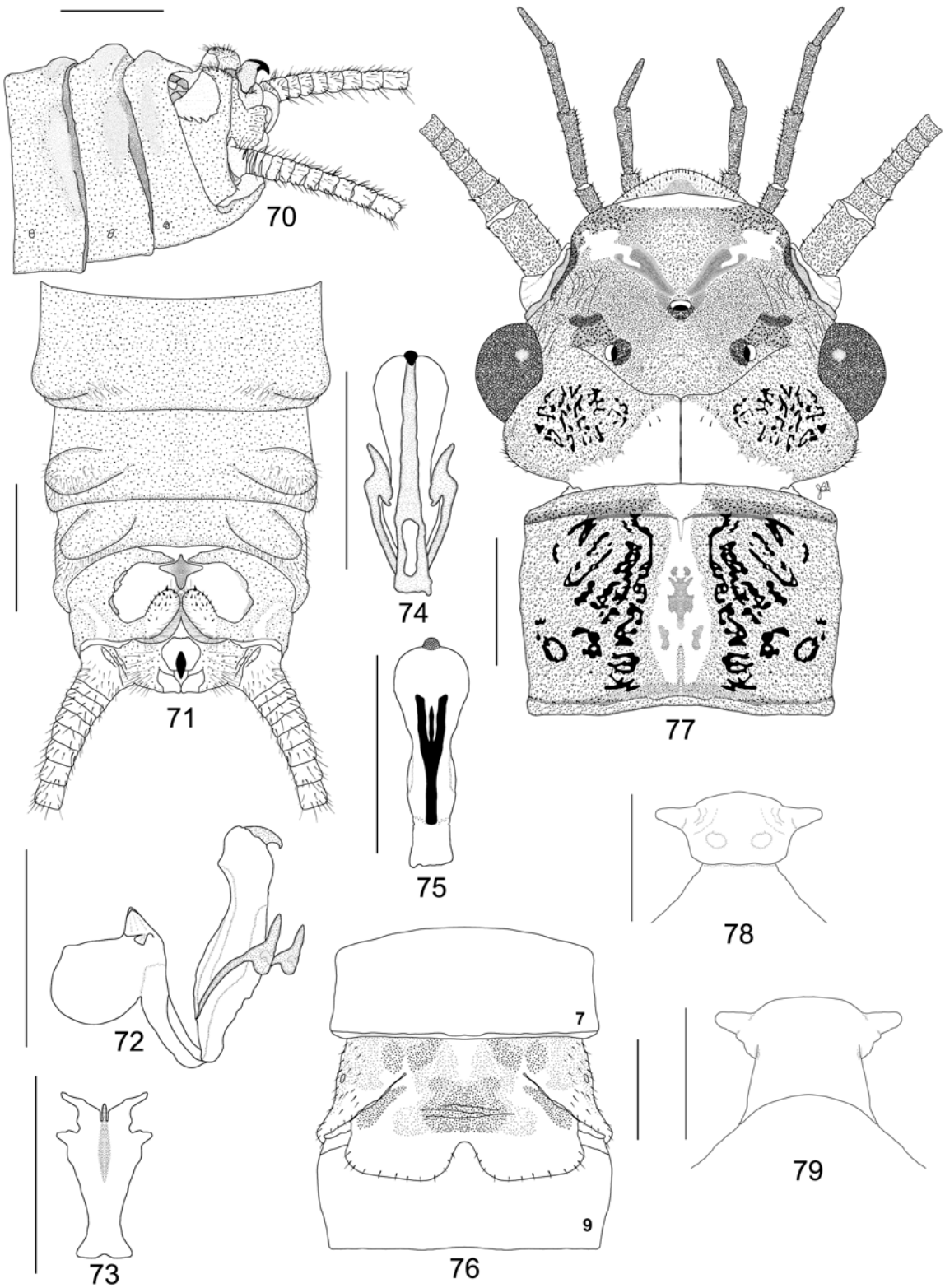
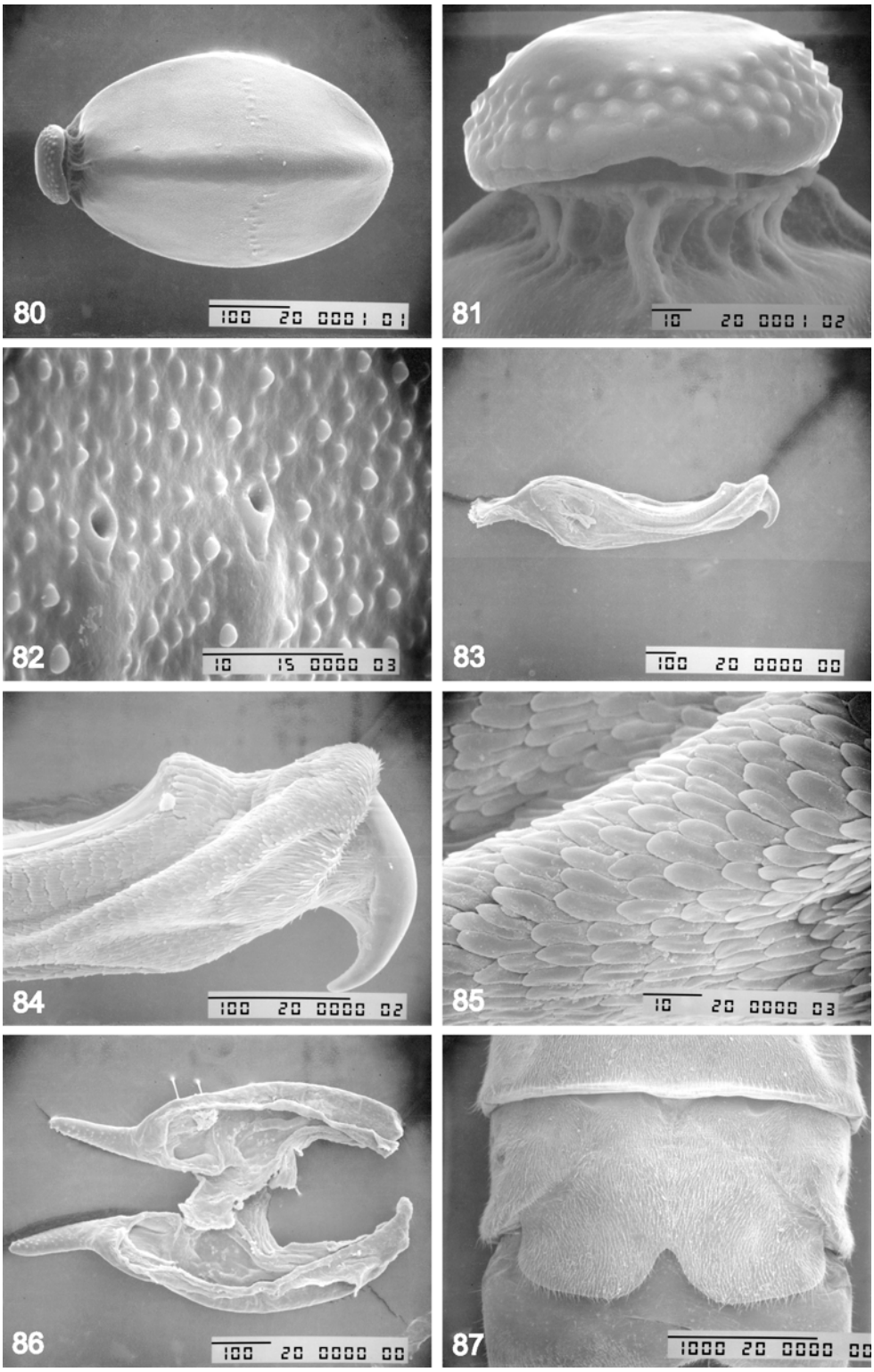


Figure 69. *Isogenoides frontalis*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 70–79. *Isogenoides frontalis*. 70. male abdomen, oblique-lateral, 25x. 71. male abdomen, non-everted, dorsal, 32x. 72. epiproct, stylets and internal basal anchor, lateral, 50x. 73. internal basal anchor, anterior, 50x. 74. epiproct and stylets, posterior, 50x. 75. epiproct, anterior, 50x. 76. female subgenital plate, sternites 7–9, 25x. 77. male head and pronotum 32x. 78. aedeagus, dorsal, 50x. 79. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 80–87. *Isogenoides frontalis*. 80. whole ova 200x. 81. detail of collar 1,000x. 82. detail of micropyles 3,500x. 83. epiproct, lateral view, 75x. 84. detail of apex 350x. 85. detail of scale-like setae 1,500x. 86. stylets, anterior view, 150x. 87. subgenital plate, segments 7-9, 35x.

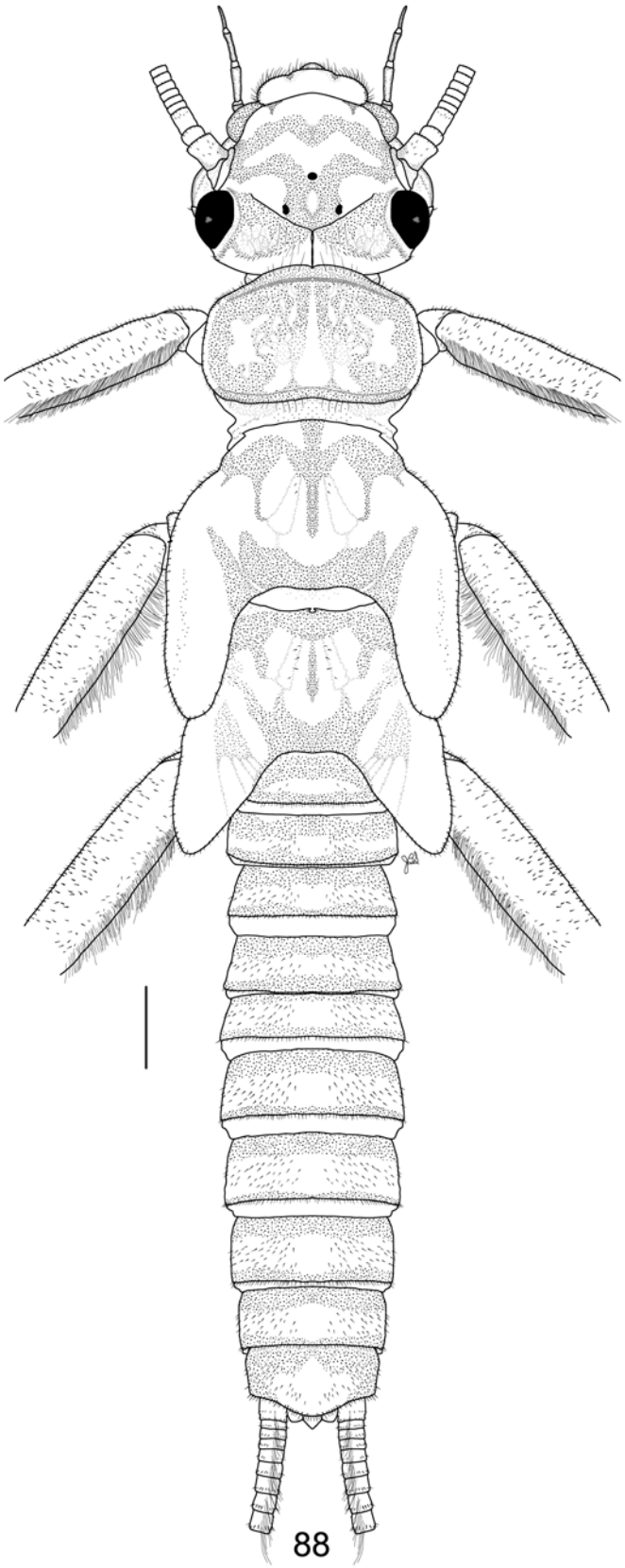
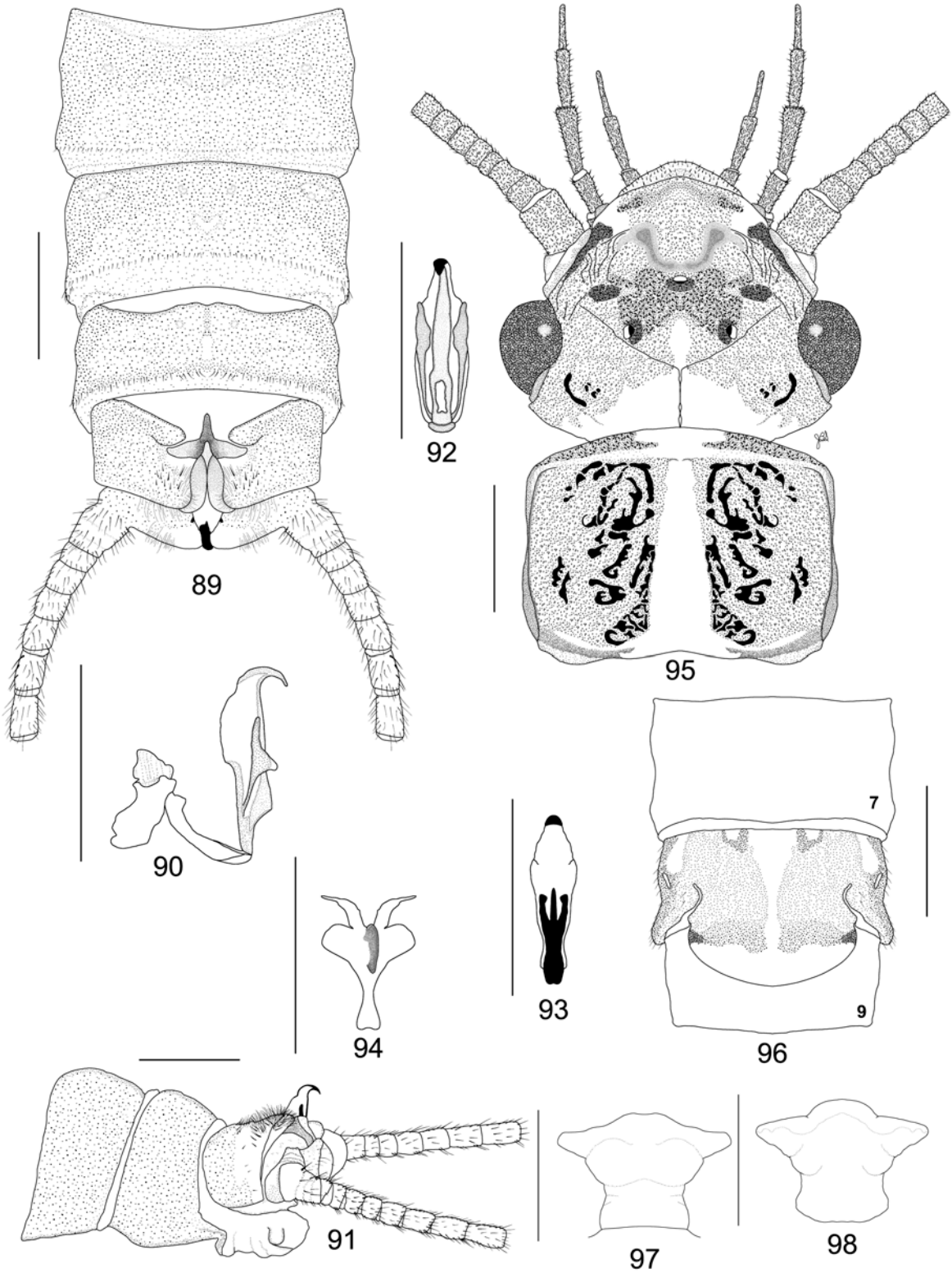
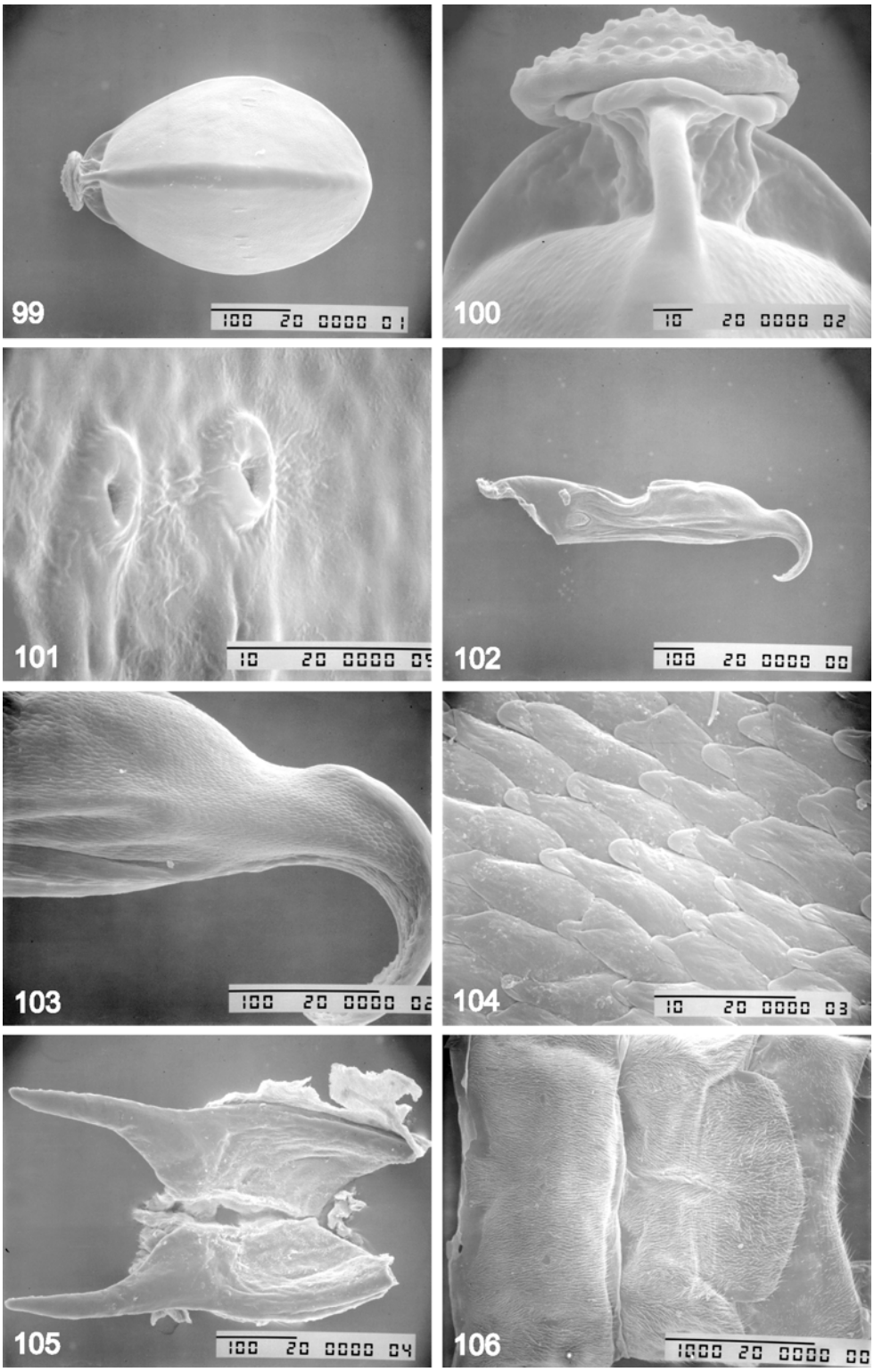


Figure 88. *Isogenoides hansoni*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 89–98. *Isogenoides hansoni*. 89. male abdomen, non-everted, dorsal, 32x. 90. epiproct, stylet and internal basal anchor, lateral, 50x. 91. male abdomen, lateral, 25x. 92. epiproct and stylets, posterior, 50x. 93. epiproct, anterior, 50x. 94. internal basal anchor, anterior, 50x. 95. male head and pronotum 32x. 96. female subgenital plate, sternites 7–9, 25x. 97. aedeagus, dorsal, 50x. 98. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 99–106. *Isogenoides hansoni*. 99. whole ova 200x. 100. detail of collar 1,000x. 101. detail of micropyles 5,000x. 102. epiproct, lateral view, 100x. 103. detail of apex 350x. 104. detail of scale-like setae 3,500x. 105. stylets, anterior view, 200x. 106. subgenital plate, segments 7-9, 35x.

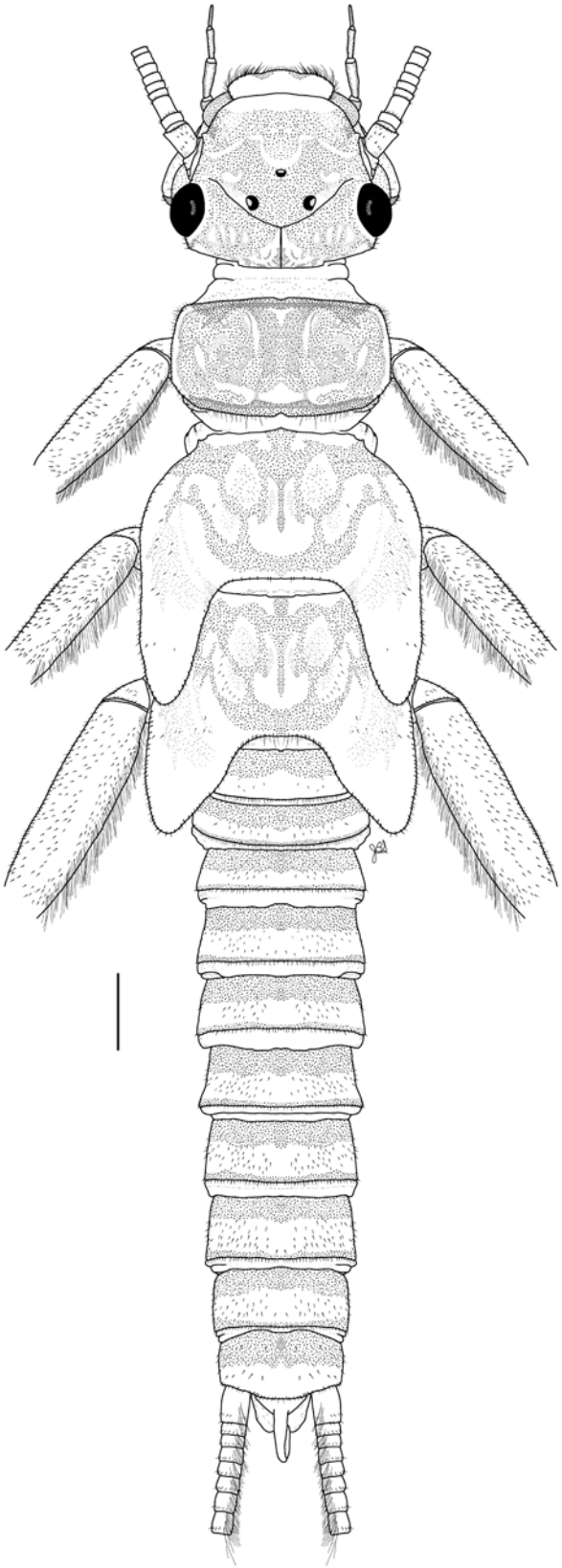


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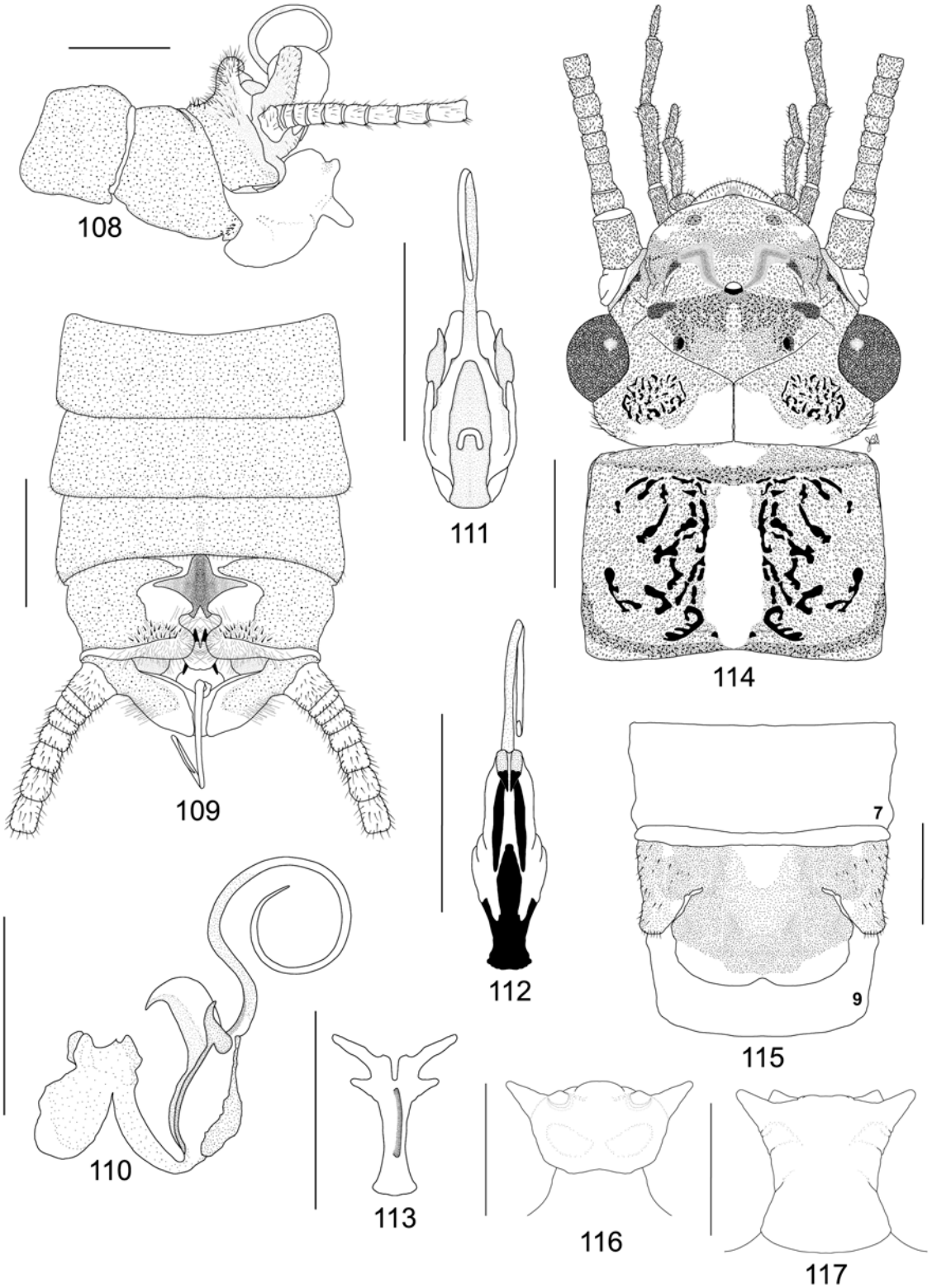
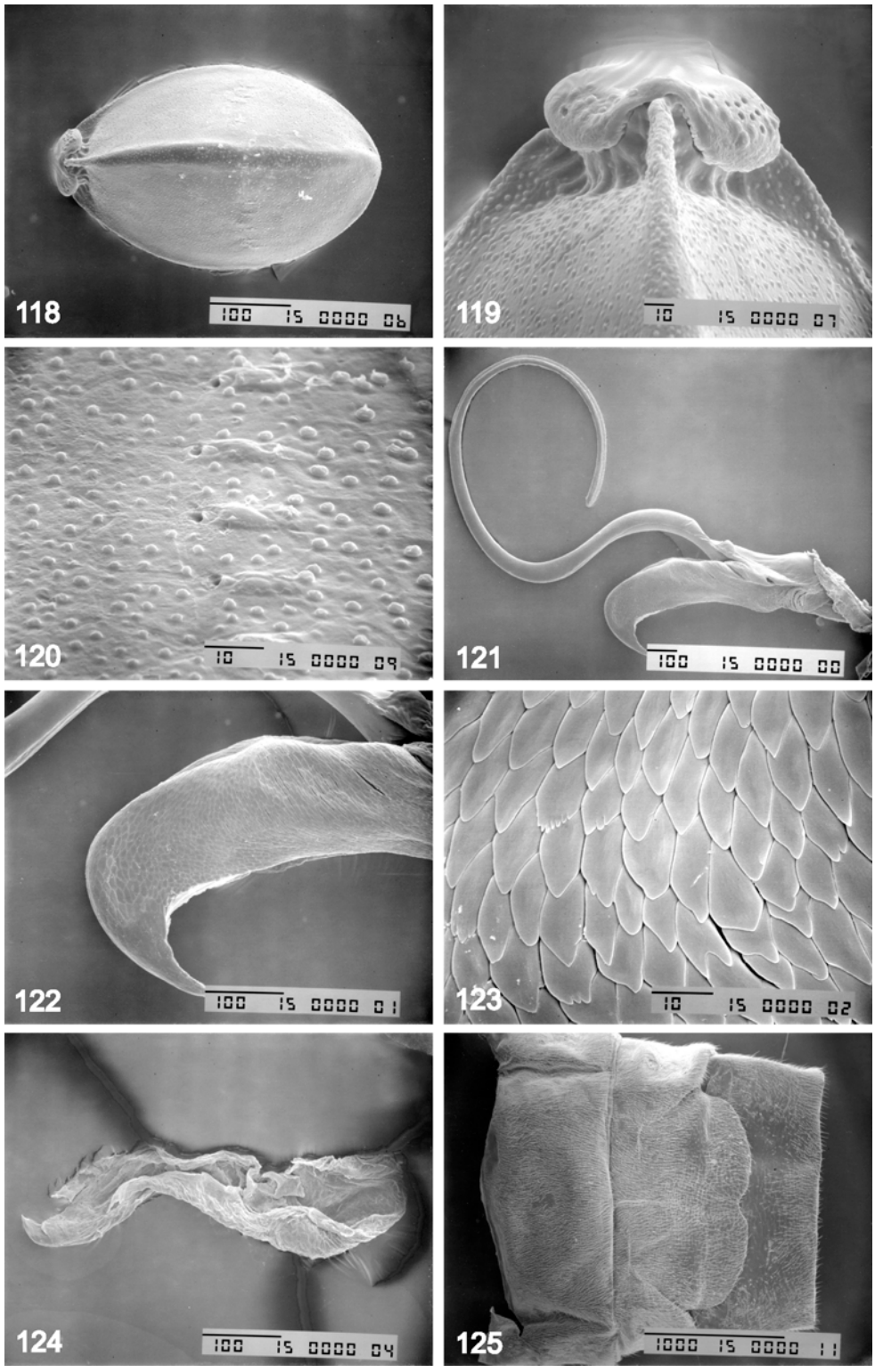
Figure 107. *Isogenoides olivaceus*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 108–117. *Isogenoides olivaceus*. 108. male abdomen, lateral, 25x. 109. male abdomen, non-everted, dorsal, 32x. 110. epiproct, stylet & internal basal anchor, lateral, 50x. 111. epiproct & stylets, posterior, 50x. 112. epiproct, anterior, 50x. 113. internal basal anchor, anterior, 50x. 114. male head & pronotum 32x. 115. female subgenital plate, sternites 7–9, 25x. 116. aedeagus, dorsal, 50x. 117. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 118–125. *Isogenoides olivaceus*. 118. whole ova 200x. 119. detail of collar 750x. 120. detail of micropyles 1,500x. 121. epiproct, lateral view, 75x. 122. detail of apex 200x. 123. detail of scale-like setae 1,500x. 124. right stylet, anterior view, 200x. 125. subgenital plate, segments 7-9, 35x.

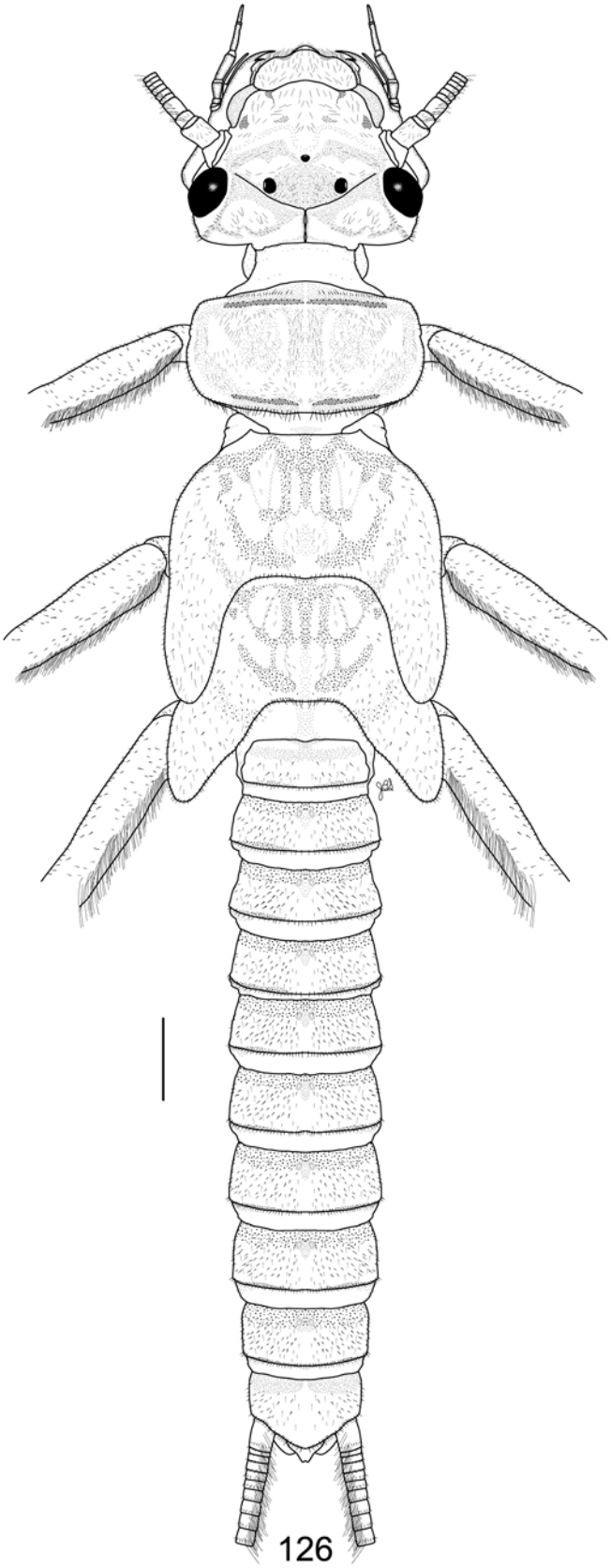
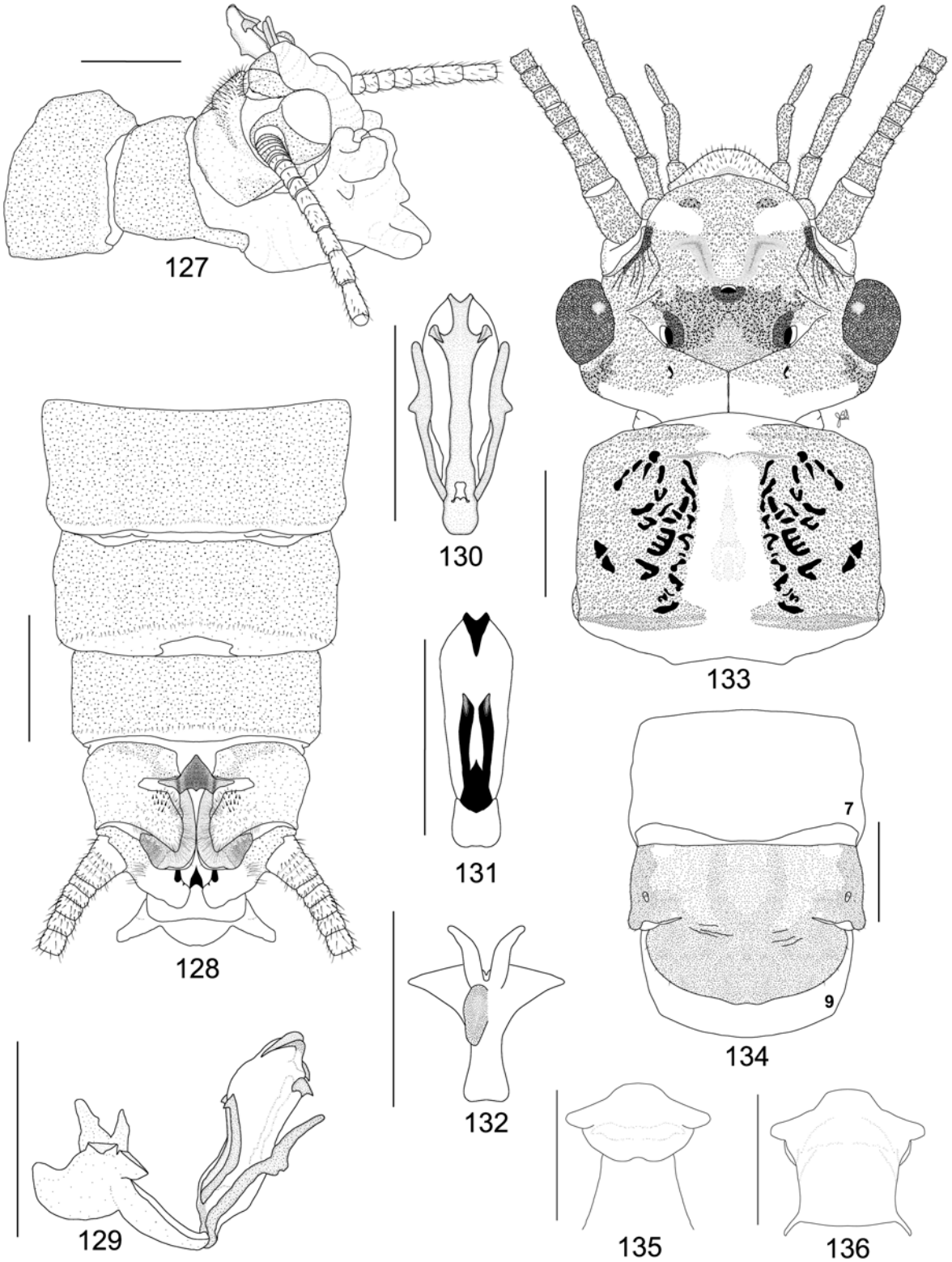
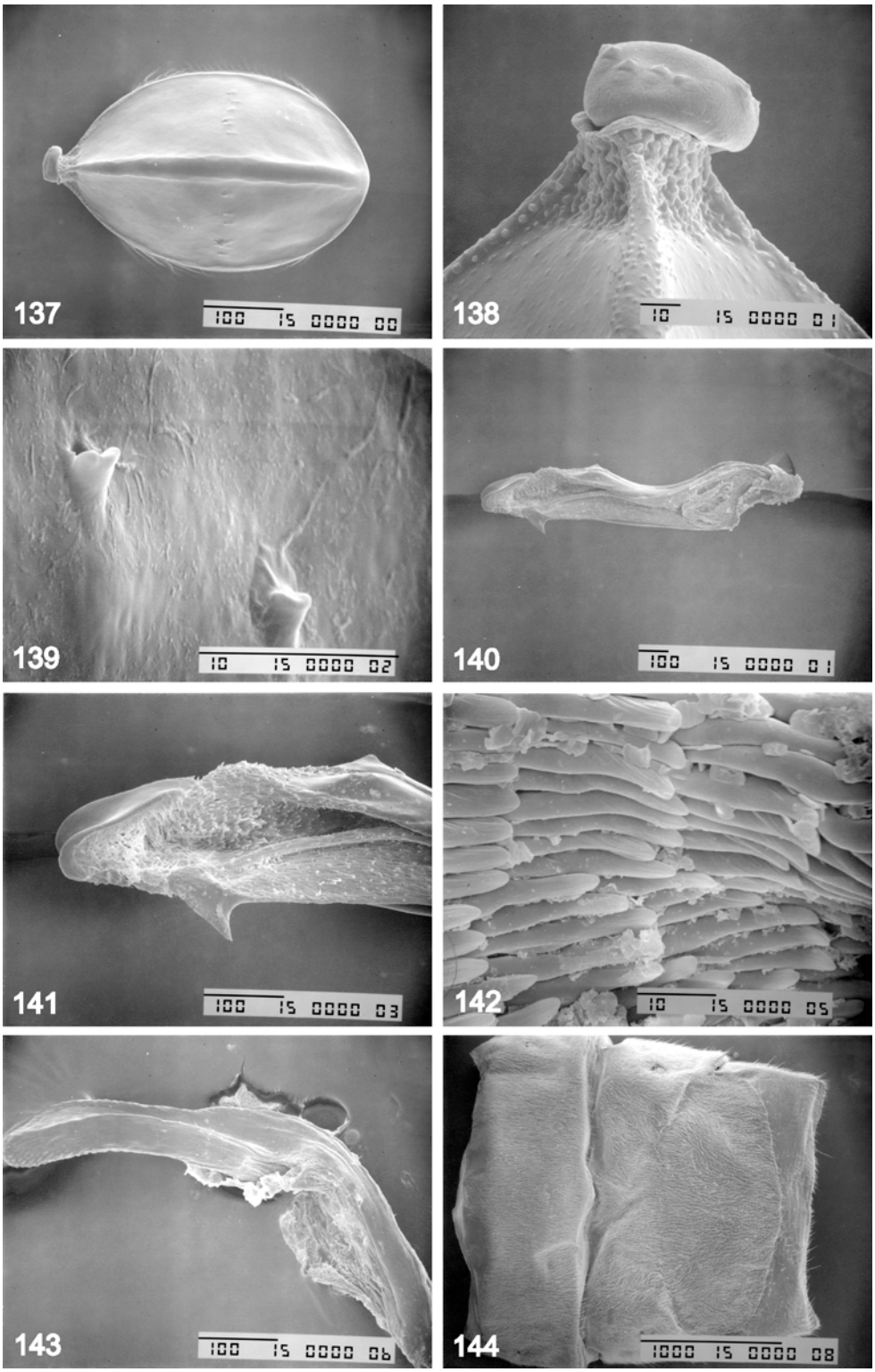


Figure 126. *Isogenoides varians*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 127–136. *Isogenoides varians*. 127. male abdomen, oblique-lateral, 25x. 128. male abdomen, everted, dorsal, 32x. 129. epiproct, stylet and internal basal anchor, lateral, 50x. 130. epiproct and stylets, posterior, 50x. 131. epiproct, anterior, 50x. 132. internal basal anchor, anterior, 50x. 133. male head and pronotum 32x. 134. female subgenital plate, sternites 7–9, 25x. 135. aedeagus, dorsal, 50x. 136. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 137–144. *Isogenoides varians*. 137. whole ova 200x. 138. detail of collar 1,000x. 139. detail of micropyles 5,000x. 140. epiproct, lateral view, 75x. 141. detail of apex 200x. 142. detail of scale-like setae 2,000x. 143. right stylet, anterior view, 200x. 144. subgenital plate, segments 7-9, 35x.

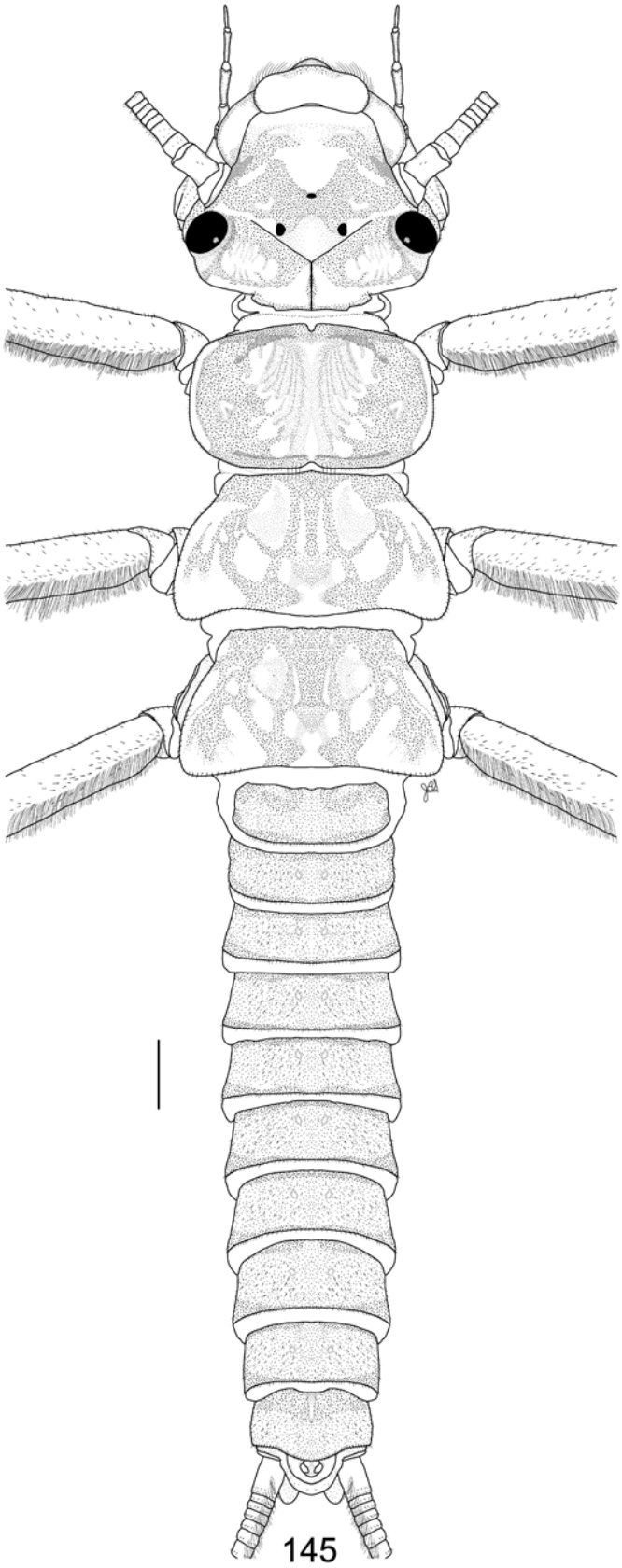
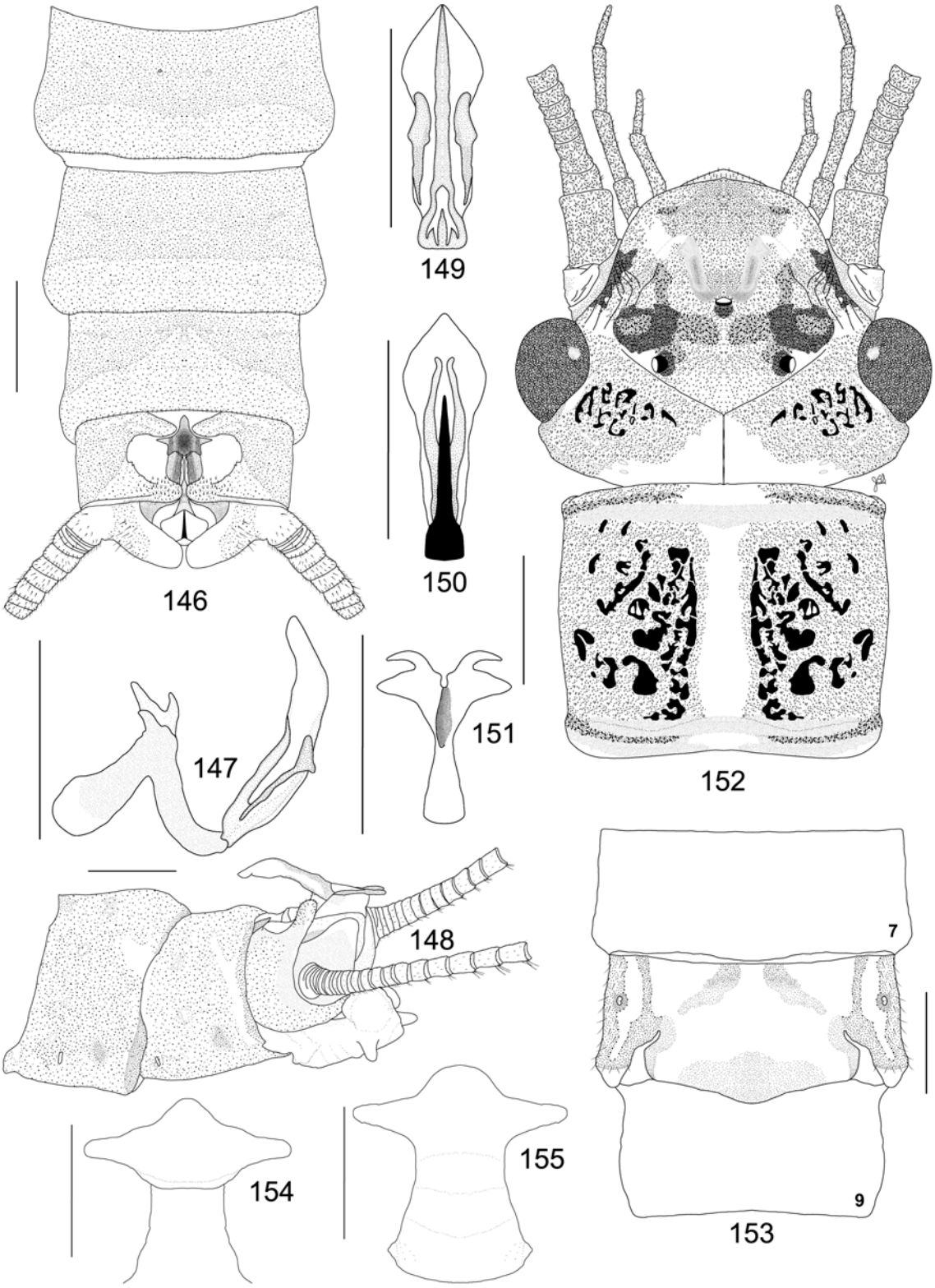
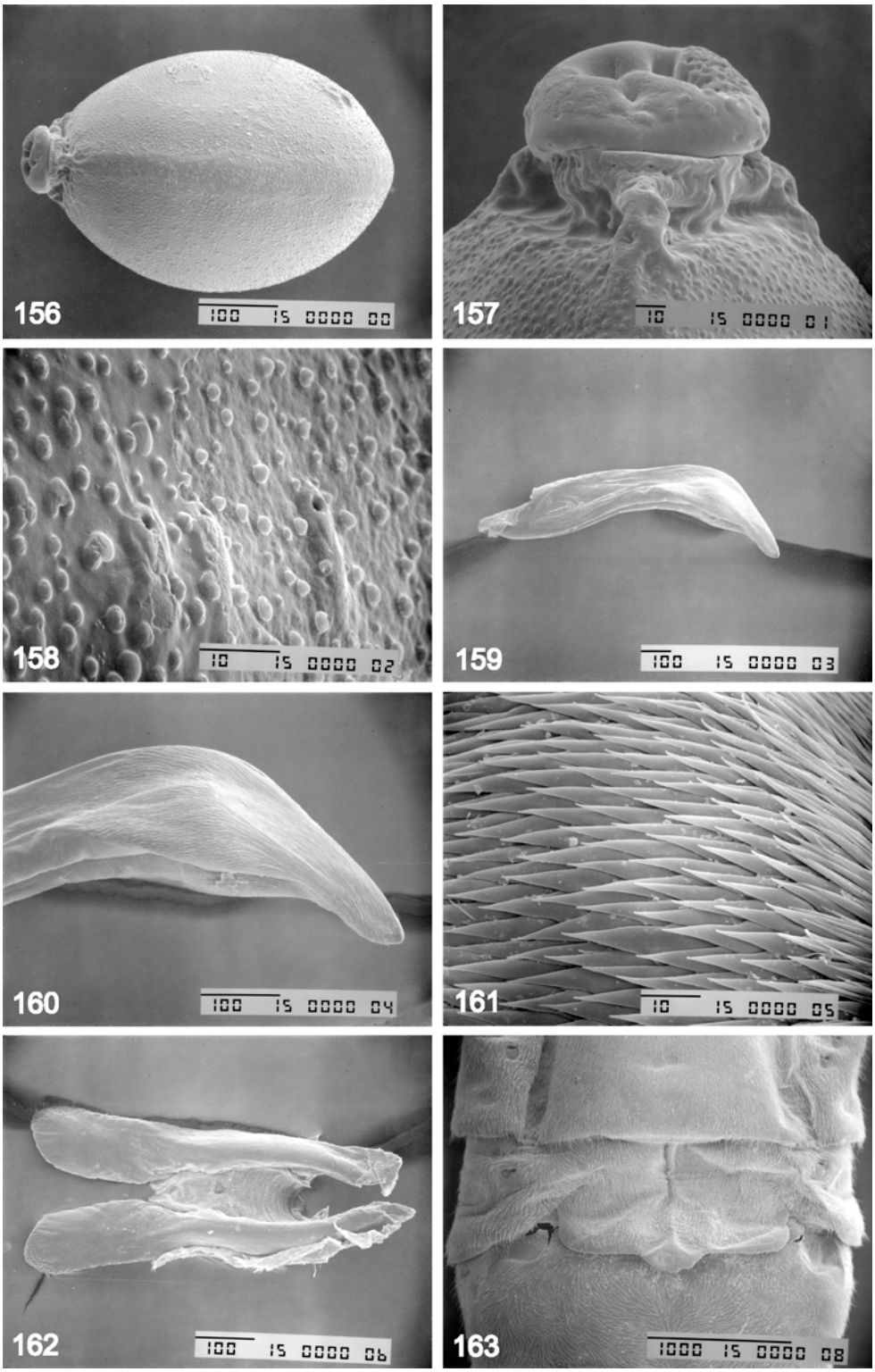


Figure 145. *Isogenoides zionensis*. Nymph habitus 25x. Scale Bar = 1mm.



Figures 146–155. *Isogenoides zionensis*. 146. male abdomen, non-everted, dorsal, 32x. 147. epiproct, stylet and internal basal anchor, lateral, 50x. 148. male abdomen, oblique-lateral, 25x. 149. epiproct and stylets, posterior, 50x. 150. epiproct, anterior, 50x. 151. internal basal anchor, anterior, 50x. 152. male head and pronotum 32x. 153. female subgenital plate, sternites 7–9, 25x. 154. aedeagus, dorsal, 50x. 155. aedeagus, ventral, 50x. Scale bars = 1mm.



Figures 156–163. *Isogenoides zionensis*. 156. whole ova 200x. 157. detail of collar 750x. 158. detail of micropyles 2,000x. 159. epiproct, lateral view, 75x. 160. detail of apex 200x. 161. detail of scale-like setae 1,500x. 162. stylets, anterior view, 150x. 163. subgenital plate, segments 7-9, 35x.

CHAPTER 3

VIBRATIONAL COMMUNICATION (DRUMMING) OF THE NEARCTIC STONEFLY GENUS *Isogenoides* (PLECOPTERA: PERLODIDAE)

Introduction

Studies over the past four decades of about 150 stonefly species from Europe, New Zealand and North America have established that the typical mating system of the northern hemisphere suborder Arctoperlaria involves a sequence of: 1, encounter site aggregation; 2, species-specific calling by males with vibrational signals, intermittent with ranging search movements; 3, duet establishment with females that become stationary; and 4, a localized search by the moving male orientating toward the female during continued duetting until location and mating are accomplished (Stewart 1994, 1997, 2001). The duetting portion of this system in stoneflies conforms generally to the review by Bailey (2003) of insect duets and their evolution, and is now considered one of the most diverse and complex known in insects.

The drumming of 53 species of the family Perlodidae, representing 20 genera, has been reported. From an evolutionary perspective (Maketon and Stewart 1988, Stewart 2001), male calls are all signaled by percussion, or in rare cases by "scratching", and span a polarity scale range from ancestral monophasy to derived group calling. The percussion in ancestral and grouped calls is done either with the non-specialized terminal-ventral abdominal sternum (*Helopicus*, *Hydroperla*, *Perlinodes*) or with specialized un-moveable posterior extensions of the abdominal sterna 7 or 8 called lobes (or "nail") in the other 17 genera (Stewart and Maketon 1991). Female answer signals in the family are predominantly monophasic answers to male calls, but

in at least *Isogenoides* species with grouped calls, they are also grouped and interspersed between the male call groups, resulting in “symphonic” duetting.

The drumming of only three *Isogenoides* species has been reported: *I. elongatus* (Hagen) (male call only, Stewart and Zeigler 1984), *I. frontalis* (Newman) (Sandberg and Stewart 2003), and *I. zionensis* Hanson (Maketon et al. 1988, Stewart and Zeigler 1984, Zeigler and Stewart 1977). Both of the *I. frontalis* and *I. zionensis* duets have been described by these authors as derived, complex symphonic conversations. The calls of *I. elongatus* described by Stewart and Zeigler (1984) appeared to be monophasic ancestral calls, but were based on only six signals from one male, therefore the authors stated that they could only be considered a preliminary characterization of the species. The objective of this study was to rear virgin males and females of all *Isogenoides* species, determine their call and answer signals and duet patterns, and examine comparatively these patterns within the genus and how they fit with the evolutionary paradigm of Stewart (2001).

Materials and Methods

Virgin adults of eight species were reared from slightly mature to mature larvae and collected as follows:

1. *Isogenoides colubrinus* (Hagen), Yampa River, At Twelvemile Gulch and Cross Canyon National Park Service area, Moffat Co., Colorado, 13/III/2002;

2. *I. doratus* (Frison), Pine River, At Walker’s Bridge, 2 mi NE. of Skookum on State Rd., Lake Co., Michigan, 11/IV/1999;

3. *I. doratus*, Rock River, At Lakewood Corner, bridge on Hwy. 75, 7.5 mi. S. of Rock Rapids, Lyon Co., Iowa, 09/II/2002;

4. *I. elongatus* (Hagen), Colorado River, Bridge on Hwy 40, 2.5 mi. W. of Granby, Garfield Co., Colorado, 01/VI/1999;

5. *I. elongatus*, Colorado River, At Rifle City Park, Garfield Co., Colorado, 12/III/2000.

6. *I. frontalis* (Newman), Rocky Run Creek, At Cty. Hwy. H, 1.5 mi. N. of Brule, Douglas Co., Wisconsin, 07/IV/2000;

7. *I. frontalis*, Cranberry River, Near intersection of Carmichael and Cranberry Rds., 3 mi. S. of Herbster, Bayfield Co., Wisconsin, 08/IV/2000;

8. *I. frontalis*, Pine Creek, At confluence of Fish Creek at Fish Cr. Rd. and Old US 2, Bayfield Co., Wisconsin, 09/IV/2000;

9. *I. hansoni* (Ricker), Stony Creek, At CR 635, 2 mi. N. of Laurel Branch confluence, Jefferson N.F., Giles Co., Virginia, 27/II/2001;

10. *I. olivaceus* (Walker), Pere Marquette River, Bridge on Hwy 37, 2.5 mi. S. of Baldwin, Lake Co., Michigan, 10/IV/1999;

11. *I. olivaceus*, Pine River, At Walker's Bridge, 2 mi NE. of Skookum on State Rd., Lake Co., Michigan, 11/IV/1999;

12. *I. varians* (Walsh), Westville Creek, Bridge on Hwy 43 at Pinola, Simpson Co., Mississippi, 12/II/2000.

13. *I. varians*, Big Otter River, Bridge on Hwy. 24 near intersection of CR 709 and CR 711, 2 mi. W. of Cambell Co., line, Bedford Co., Virginia, 26/II/2001;

14. *I. zionensis* Hanson, San Miguel River, Near Placerville, San Miguel Co., Colorado, 13/VI/1999.

Drumming signals were recorded with a marantz® portable cassette recorder, Model PMD-430) (D&M Holdings, Kangawa, Japan, http://www.dm-holdings.com/) and

SONY® electret condenser microphones, Model ECM95S, (Sony Corporation, Tokyo, Japan, http://www.sony.net/SonyInfo/CorporateInfo.com/) or with a Sony® MiniDisc portable recorder Models MZ-R37 or MZ-R700 and omnidirectional microphones in a 2-compartment, glass covered field recording chamber (Stewart and Sandberg 2004, Sandberg and Stewart 2003). Recorded signals were digitally encoded and analyzed using the methods provided in (Sandberg and Stewart 2003).

Results

Isogenoides colubrinus One hundred fifteen and 114 signals were obtained from five 1-6 day old males and four females, respectively, at 20-28ºC, or normal incandescent or florescent room lights (Provo, Utah and Brighton, Colorado), and partially shaded sunlight near mountain streams (Leopard Creek and Mosquito Creek, Colorado). Their exchanges were complex, ranging from 3-way call-answer-response sequences (N=12) (Fig. 1A), to grouped calls with grouped, interspersed female answers (Fig. 1B). Typically, the grouped exchanges involved a short symphony of about three ♂-♀ volleys, terminated by a slow (wider-interval) male response signal (♂ response symbol underlined in figures). Females did not always intersperse an answer between every male call group and two exchanges lacked the terminal response group.

The male sequenced and grouped calls consisted of five mode beats (5.2 ± 0.7) with intervals of 65.0 ± 8.3 msec (Table 1). These expressions [examples: (5.2 ± 0.7) and 65.0 ± 8.3 msec] represent a $\bar{x}$ ± standard deviation and will be used as such throughout the rest of this paper. Only 10 symphonies possessed male call groups with seven beats, all others ranged from 3-6. The number of call groups ranged from 1-7 with individual mean interbeat intervals (interval 1 (i1) – interval 6 (i6)) generally

increasing, early intervals increased slightly in approximate 3-msec increments from 59.7 ± 7.8 msec (1st) to 72.6 ± 9.0 msec (5th) (Table 2). The last mean interbeat interval decreased to 69.4 ± 5.7 msec, which may be suspect due to small sample size (N=10).

Mode and mean number of beats per interspersed female answer signals were 1 and 1.8 ± 0.8 msec (Table 1). Average interbeat intervals increased throughout the answer and overall they were 121.8 ± 26.8 msec. In duets and symphonies, female answers followed male call groups (♂-♀ exchange interval) by 402.0 ± 101.2 msec and subsequent male calls followed female answer groups (♀-♂ exchange interval) by 1654.8 ± 429.1 msec. The terminal male response signal was different from sequenced and grouped calls with a mode beat count of 2 (2.5 ± 0.9) and interbeat intervals of 441.8 ± 142.5 msec (Table 1). Mean intervals of the response decreased from 452.4 ± 136.2 msec (1st) to 384.0 ± 135.5 msec (4th), the last interval increased to 462.5 ± 147.8 msec, which may be suspect due to small sample size (N=2). The last (♀-♂) exchange interval was 626.4 ± 198.5 msec.

Isogenoides doratus Two populations were recorded in 1999 and 2002, from Michigan and Iowa respectively. The Michigan tests included 126 exchanges obtained from one, 1-9 and 1-12 day old male and female respectively, at 24ºC, and 88 foot-candles (FTC). Their exchanges were grouped male calls with interspersed female answers (Fig.2A). Typically, the exchanges involved long symphonies of about ten ♂-♀ grouped signals that ended either with an unanswered male call group or with a female answer signal. Males did not end exchanges with response signals and females did not always intersperse an answer between every male call.

The Michigan male call groups consisted of three mode beats (3.1 ± 0.6) with intervals of 16.7 ± 3.0 msec (Table 1). Only nine symphonies possessed male call groups with five beats, all others ranged from 1-4. The number of call groups ranged from 2-21 with individual mean interbeat intervals (i1 – i4) generally decreasing with irregular intervals (Table 2) from 17.5 ± 2.1 msec (1^{st}) to 10.1 ± 1.8 msec (3^{rd}). The last interval increased slightly, which may be suspect due to small sample size.

Mode and mean number of beats per interspersed female answer signals were 2 and 2.1 ± 1.0 (Table 1). Average interbeat intervals increased throughout the answer and overall they were 107.0 ± 52.0 msec. In symphonies the (♀-♂) exchange interval was 699.4 ± 170.0 msec. Females began their grouped answer signals only after the second male call-group and the (♂-♀) exchange interval was 466.4 ± 89.4 msec.

The Iowa tests included 115 exchanges obtained from four and six, 2-7 day old males and females respectively, at 24ºC, and 80-88 FTC. Their exchanges were grouped male calls with interspersed female answers (Fig. 2B) and similar to Michigan exchanges. Typically, the exchanges involved long symphonies of either about seven ♂-♀ signals that ended with an unanswered male call group or with a female answer signal. Males did not end exchanges with response signals and females did not always intersperse an answer between every male call.

The Iowa male call groups consisted of three mode beats (3.1 ± 1.2) with intervals of 14.4 ± 3.8 msec (Table 1). Only six and one symphonies possessed male call groups with seven and eight beats respectively, all others ranged from 1-6. This increased beat-resolution over the Michigan tests may be attributed to our then-new digital recording methods and minor changes made to the recording chamber. The

number of call groups ranged from 2-22 with individual mean interbeat intervals (i1 – i7) decreasing unevenly (Table 2) from 16.7 ± 2.2 msec (1^{st}) to 6.5 ± 1.3 msec (6^{th}). The last interval increased, and may be suspect due to small sample size.

Mode and mean number of beats per interspersed Iowa-female answer signals were 1 and 1.5 ± 0.7 (Table 1). Average interbeat intervals decreased until the penultimate (4^{th}) interval, then increased slightly during the 5th interval and overall they were 135.5 ± 40.7 msec, which is notably larger than Michigan average answer intervals. This unexplained decreasing interval pattern for Iowa females is opposite to the Michigan females. In symphonies the (♀-♂) exchange interval was 724.8 ± 169.2 msec. Females began their grouped answer signals after the second male call group, except one exchange, where the female answered the male's first call and the (♂-♀) exchange interval was 358.7 ± 79.9 msec. I propose, with the exceptions of overall average female interbeat interval, and opposite female answer interval patterns, that these two *I. doratus* populations compared well. Male mode and average number of beats and overall mean beat interval overlapped sufficiently.

Isogenoides elongatus Two Colorado populations were recorded in 1999 and 2000 from two different sampling sites on the Colorado River, the first near Granby and the second at Rifle respectively. The Granby tests included 160 signals obtained from seven and three field collected males and females respectively, at 18-21ºC, and normal incandescent room lighting in Pitkin, Colorado. The age of these individuals was unknown but assumed old because kick net sampling for nymphs was unsuccessful and no other adults were observed in usual habitats.

The Granby drumming exchanges were complex, ranging from 2- and 3-way call-answer-response sequences (Figs. 3A and 3B), to grouped calls with grouped, interspersed female answers (Fig. 3C). Typically, the sequences involved a single ♂-♀ volley that sometimes ended with a slower (1-2 beat) male response signal. Females always interspersed an answer between every male call group and 111 duets lacked the slow male response signal.

The Granby sequenced and grouped male calls consisted of seven mode beats (6.8 ± 1.1) with intervals of 397.0 ± 75.0 msec (Table 1). Only six exchanges possessed male first call groups with 9-beats and one with 10-beats, all other male call groups ranged 3-8 beats. The number of call groups ranged from 1-3 with individual mean interbeat intervals (i1 – i9) increasing unevenly (Table 2) from 354.4 ± 51.8 msec (1^{st}) to 472.8 ± 88.5 msec (8^{th}). The last mean interbeat interval increased noticeably to 638.3 ± 44.6 msec, and may be suspect due to small sample size.

Mode and mean number of beats per sequenced and interspersed Granby female answer signals were 3 and 2.5 ± 0.6 msec (Table 1). Average interbeat intervals increased throughout the answer and overall intervals were 386.9 ± 93.7 msec. In sequenced and grouped exchanges, the (♂-♀) exchange interval was 925.5 ± 286.0 msec. The terminal male response signal was different from calls with a mode beat count of 1 (1.1 ± 0.3) and mean interbeat intervals of 760.8 ± 222.7 msec (Table 1). The (♀-♂) exchange interval was relatively even throughout exchanges with an average of 1971.9 ± 159.8 msec. The last of these (♀-♂) exchange intervals, before the male response signal, decreased to 888.8 ± 294.8 msec.

The Rifle drumming exchanges were also complex, ranging from 2- and 3-way call-answer-response sequences to grouped calls with grouped, interspersed female answers (Fig. 3D). Typically, the sequences involved a single ♂-♀ volley that sometimes ended with a 1-beat male response signal (Table 1). Females did not always intersperse an answer between every male call group and 64 duets lacked the slow male response signal.

The Rifle sequenced and grouped male calls consisted of six mode beats (5.9 ± 0.7) with intervals of 222.1 ± 14.0 msec (Table 1). These call intervals were noticeably smaller than Granby call intervals and may be attributed to the assumed increased age of the Granby test pairs. Only one exchange possessed a first call group with 8-beats, all other male call groups ranged 4-7 beats. The number of call groups ranged from 1-3 with individual mean interbeat intervals (i1 – i7) increasing unevenly (Table 2) from 207.5 ± 17.9 msec (1^{st}) to 229.2 ± 9.0 msec (4^{th}). Interval 5 decreased slightly (228.0 ± 8.8 msec), then increased irregularly to the last interval (7^{th}) 242.1 msec (N=1). The interval pattern in general increased from the first to last beats for both populations (Table 2). Incremental interval increase appeared to be greatest at the beginning and ending of average sequenced and grouped calls with less incremental increase in middle intervals (Table 2).

Mode and mean number of beats per sequenced and interspersed Rifle female answer signals were 2 and 1.8 ± 0.5 msec (Table 1). Average interbeat intervals increased throughout the answer and overall they were 180.5 ± 20.7 msec. However, these intervals were shorter than the Granby population and assumed to be so because of their younger age. In sequenced and grouped exchanges, the (♂-♀) exchange

interval was 570.0 ± 82.1 msec and the terminal male response signal was different from calls with a mode beat count of 1 (Table 1). The (♀-♂) exchange interval was relatively even throughout exchanges with an average of 950.2 ± 124.1 msec. The last (♀-♂) exchange interval decreased to 648.3 ± 178.6 msec.

In agreement with (Stewart 1997), male-call beat and interval data convey the critical information of species specificity, possible reproductive fitness, and phylogenetic information. Therefore the two *I. elongatus* populations agree with one another in terms of the male call interval description (Table 2). The major differences were the Granby males and females increased beat intervals that are assumed the result of their increased age.

Isogenoides frontalis One hundred thirty-five exchanges were obtained from ten, 1-2 day old males and four females, respectively, at 23-24ºC, and 84 FTC. Their exchanges were complex, ranging from 3-way call-answer-response sequences (Fig 4A) to grouped calls with grouped, interspersed female answers (Fig. 4B). Typically, the grouped exchanges involved a short symphony of about three ♂-♀ signals, terminated by a slow male response signal. Females did not always intersperse an answer between every male call group and three duets lacked response signals.

The male sequenced and grouped calls consisted of four mode beats (4.1 ± 0.7) with intervals of 61.2 ± 11.3 msec (Table 1). Only one symphonic exchange possessed a male group with six beats, all other male call groups ranged 2-5 beats. The number of call groups ranged from 1-6 with individual mean interbeat intervals (i1 – i5) generally increasing at approximate 8-msec increments (Table 2), from 51.9 ± 8.4 msec (1^{st}) to

77.3 ± 8.3 msec (4th). The last interval decreased to 65.5 msec (N=1) that may be considered suspect due to small sample size.

Mode and mean number of beats per interspersed female answer signals were 2 and 1.6 ± 0.6 msec (Table 1). Average interbeat intervals decreased throughout the short answers and overall they were 93.8 ± 29.3 msec. In symphonic exchanges, the (♂-♀) exchange interval was 581.5 ± 76.3 msec and the terminal male response signal was different from call groups with a mode beat count of 3 (3.5 ± 1.5) and interbeat intervals of 288.8 ± 129.4 msec. (Table 1). Mean intervals of the response increased from 251.8 ± 114.3 (1st) to 446.2 msec (N=1) (7th), the sixth interval decreased to 297.0 ± 38.7 msec and these last two intervals may be suspect due to small sample size (N=4).

Isogenoides hansoni Sixty signals were obtained from four, 2-5 day old males at 22-24ºC, and 70 FTC. Their calls were grouped signals with rapid interbeat intervals and short resting intervals between groups (Fig. 5). Typically, the first group contained more beats than the last two, with greatest interval variation within the first five beats. Female nymphs collected at the same time as males (February) failed to emerge successfully (April) under prolonged simulated-stream laboratory conditions.

The male grouped calls consisted of six mode beats (9.3 ± 4.3) with intervals of 31.3 ± 9.4 msec (Table 1). Only four calls possessed groups with beat counts of 19, all other ranged from 5-18. All male calls contained three groups with individual average interbeat intervals (i1 – i18) generally decreasing (Table 2) from 35.0 ± 13.8 msec (1st) to 29.0 ± 5.4 msec (6th), then remaining approximately even over intervals 7-11 with irregular increases and decreases of 0.2–0.9 msec. A decreasing interval pattern was

again observed from the (12th) 28.8 ± 2.1 msec to the (17th) 25.0 ± 4.0 msec (N=11). The last interval increased slightly to 25.6 ± 1.2 msec, which may be suspect due to small sample size. The intervals between male calls (♂-♂ exchange interval) remained approximately even at 259.2 ± 21.1 msec and average beat counts decreased, the first group with 14.2 ± 2.7, the second with 7.3 ± 0.7, and the last with 5.8 ± 0.6. The average interbeat intervals for each group overall decreased from 33.0 ± 12.3 msec (1st) to 28.8 ± 2.1 msec (2nd), and then increased slightly to 29.9 ± 2.1 msec (3rd).

Isogenoides olivaceus Two hundred sixty-nine signals were obtained from two 2-12 day old males and seven females, respectively, at 20-24ºC, and 74 FTC. Their exchanges were mostly simple, ranging from 2-way (Fig. 6A) to 3-way call-answer-response sequences (Fig. 6B). Only one grouped 7-way exchange (Fig. 6C) was recorded over an eleven-day drumming period. Typically, the sequences involved a single ♂-♀ volley that sometimes (N=88) ended with a slower male response signal.

The male sequenced calls consisted of seven mode beats (6.7 ± 0.5) with intervals of 98.2 ± 12.0 msec (Table 1). Only three male-calls possessed call groups with 8-beats, all others ranged from 5-7. The number of call groups ranged from 1 (N=269) to 3 (N=1), with individual sequenced mean interbeat call intervals (i1 – i7) decreasing irregularly (Table 2) from 107.0 ±12.0 ms (1st) to 85.8 ± 8.2 ms (7th). Average incremental interval decreased slowly during the first three intervals, then rapid during intervals 4 and 5, and finally slow again over the remaining intervals (Table 2).

Mode and mean number of beats per sequenced female answer signals were 6 and 5.5 ± 1.7 msec (Table 1). Average interbeat intervals increased from 74.9 ± 16.4 msec (1st) to 115.1 ± 32.9 msec (7th), decreased slightly at the penultimate (8th) interval

(113.5 ± 37.2 msec), and then increased to 126.0 ± 66.7 msec (9th), and overall they were 86.6 ± 22.0 msec. In sequences, the (♂-♀) exchange intervals were 739.9 ± 130.9 msec and (♀-♂) exchange intervals were 831.6 ± 231.1 msec. The terminal male response signal was different from calls with a mode beat count of 1 (1.9 ± 1.0) and interbeat intervals increased from 340.2 ± 143.9 msec (1st) to 517.0 (N=1) (5th).

Isogenoides varians Two populations were recorded in 2000 and 2001, from Mississippi and Virginia respectively. The Mississippi tests included 125 signals from four 4-10 day old males and four females respectively, at 20-24ºC, and 74 FTC. One recorded female did not answer the calls of two different males. Their exchanges were complex, ranging from 3-way call-answer-response sequences (N=3), to grouped calls with grouped, interspersed female answers (Fig. 7A). Typically, the grouped exchanges involved a short symphony of about three ♂-♀ volleys, terminated by a slow male response signal. Females did not always intersperse an answer between every male call and only answered the first-male call group in four exchanges. Males did not always end sequenced or grouped exchanges with the slow response group.

The Mississippi male sequenced and grouped calls consisted of six mode beats (6.5 ± 1.6) with intervals of 26.7 ± 3.1 msec (Table 1). Only four symphonies possessed male calls with 10 beats, all others ranged from 2-9. The number of male sequenced and grouped calls ranged from 1-7 with individual mean interbeat intervals (i1 – i9) increasing slightly with small average incremental changes (Table 2) from 25.8 ± 3.7 msec (1st) to 28.0 ± 2.9 msec (6th and 7th), decreasing slightly to 27.1 ± 2.2 msec (8th), then finally increasing again to 30.0 ± 1.6 msec (9th). The last interval may be suspect due to small sample size.

Mode and mean number of beats per interspersed Mississippi female were 4 and 3.4 ± 1.0) (Table 1). Average interbeat intervals increased throughout the answer and overall they were 52.4 ± 9.2 msec. The (♂-♀) exchange interval was 944.8 ± 64.0 msec and the (♀-♂) exchange interval was 1285.7 ± 276.3 msec. The terminal male response signal was different from sequenced and grouped calls with a mode beat count of 3 (3.2 ± 1.3) and interbeat intervals of 56.0 ± 11.8 msec (Table 1). Mean male response intervals increased from 53.5 ± 11.7 msec (1^{st}) to 59.3 ± 11.1 msec (4^{th}), and then decreased to 46.6 ± 3.6 msec and 47.7 msec (5^{th} and 6^{th} respectively) that may be suspect due to small sample size (N=3).

The Virginia tests included 117 signals obtained from four 1-12 day old males and two females respectively, at 24ºC, and 76 FTC. Their exchanges were complex and ranged from 2-way (N=2) and 3-way (N=4) call-answer-response sequences to grouped calls with grouped, interspersed female answers (Fig. 7B). Typically, the grouped exchanges involved a short symphony of about three ♂-♀ volleys, terminated by a slow male response signal. Females did not always intersperse an answer between every male call and only answered the first-male call group in seventeen exchanges. Males did not always end sequenced or grouped exchanges with the slow response group.

The Virginia male sequenced and grouped calls consisted of eight mode beats (7.1 ± 1.5) with intervals of 36.9 ± 4.0 msec (Table 1). Only five symphonies possessed male call groups with 10 beats, and two with 11 beats, all others ranged from 2-9. The number of male sequenced and grouped calls ranged from 1-6 with individual mean interbeat intervals (i1 – i10) slightly increasing (Table 2) with small interval changes

from 35.4 ± 4.5 msec (1st) to 41.7 ± 5.0 msec (8th), decreasing to 40.2 ± 5.3 msec (9th), then finally increasing to 44.4 ± 2.2 msec (10th). The last three call-intervals may be suspect due to smaller sample size.

Mode and mean number of beats per interspersed Virginia female were 2 and 2.4 ± 0.9 (Table 1). Average interbeat intervals increased from 52.6 ± 7.1 msec (1st) to 70.4 ± 11.0 msec (3rd), and then decreased to 58.6 msec (N=1). This last interval may be suspect due to small sample size. The (♂-♀) exchange interval was 839.9 ± 61.4 msec and the (♀-♂) exchange interval was 1279.4 ± 305.2 msec. The terminal male response signal was different from sequenced and grouped calls with a mode beat count of 3 (3.1 ± 0.9) and interbeat intervals of 73.4 ± 21.4 msec (Table 1). Mean male response intervals increased from 63.7 ± 11.1 msec (1st) to 94.2 ± 35.8 msec (3rd), and then decreased to 71.8 msec (N=1). This last interval is suspect due to small sample size.

The differences in mode male number of beats and overall male call interbeat interval are substantial and suggest that these *I. varians* populations may have unique drumming dialects. Differences could also be the result of unknown local environmental variables, such as temperature, atmospheric pressure, or light intensity. Another possibility for difference is that these two populations may be changing and one may become a potentially behaviorally cryptic species (Sandberg and Stewart 2003).

Isogenoides zionensis Three hundred and seven signals were obtained from seven 2-5 day old males and nine females respectively, at 21-22ºC, and normal room lighting in Pitkin, Colorado. Their exchanges were complex and ranged from 2- or 3-way call-answer-response sequences (Fig. 8A), to grouped calls with grouped,

interspersed female answers (Fig. 8B). A third and more complex drumming exchange type was observed (N=21) where males linked together two or more simple call-answer-response sequences by beginning their next call series within or soon after the otherwise terminal response signal (Fig. 8C). Usually (less complex sequenced and grouped exchanges), after sending the terminal response sequence, males began moving (localized search behavior) for variable lengths of time, while females remained stationary, and then after searching, continued with new call signal. Several exchanges containing these (male response-male call) variable series show a decreasing trend, shortening the time lag between the male response and next call. Therefore, these complex ♂-♀ exchanges contained series of grouped or sequenced, or both grouped and sequenced exchange types. Typically, grouped exchanges involved a short symphony of about four ♂-♀ volleys, terminated by a slow male response signal. Females did not always intersperse an answer between every male call group and males did not always end sequenced or grouped exchanges with the slow response group.

In complex series where male response signals were linked to the following male call signals, the average ♂ (call) - ♂ (response) exchange intervals were 458.3 ± 248.7 msec. These intervals were shorter than the ♂ (call) -♂ (call) exchange intervals between grouped and unanswered male call groups and were 1083.5 ± 266.8 msec.

The less-complex male sequenced and grouped calls consisted of four mode beats (4.0 ± 0.6) with intervals of 364.3 ± 59.1 msec (Table 1, first entry). Only one sequence possessed a male call group with six beats, all others ranged from 1-5. The number of call groups ranged from 1-3 with individual mean interbeat intervals (i1 – i5)

generally switching from increasing to decreasing (Table 2, first entry). Intervals increased from 337.6 ± 71.0 msec (1st) to 380.3 ± 46.8 msec (3rd), and then decreased noticeably to 359.8 ± 25.8 msec (4th). The final interval decreased to 344.4 msec, which may be suspect due to small sample size. However, in terms of both sample size and amount of change, I interpret this as the first switching interval pattern observed in *Isogenoides* male call groups (Table 2, first entry). All other *Isogenoides* individual call intervals generally increased or decreased.

Mode and mean number of normal sequenced or interspersed female answer signals were 2 and 2.2 ± 1.1 msec (Table 1, first entry). Average interbeat intervals increased throughout the answer and overall they were 136.8 ± 32.7 msec. In symphonies, the (♂-♀) exchange intervals were 624.3 ± 129.3 msec and the (♀-♂) exchange intervals were 561.2 ± 197.3 msec. The terminal male response signals were different from sequenced and grouped calls with a mode and mean beat count of 3 (3.7 ± 1.4) and interbeat intervals of 132.2 ± 43.4 msec. Mean intervals of the response increased from 107.4 ± 24.6 (1st) to 198.5 ± 56.9 msec (5th).

Twenty-one complex signals were obtained from two and five males and females respectively, under the same conditions as above. Their exchanges were the most complex observed in *Isogenoides* where the typical series was usually a grouped exchange type that involved a call-answer-response-call pattern as described above.

The more-complex male calls consisted of four mode beats (3.6 ± 1.1) with intervals of 344.8 ± 32.2 msec (Table 1, second entry). Only two series possessed call groups with six and seven beats respectively, all others ranged from 1-5. The number of call groups ranged from 2-6 with individual mean interbeat intervals (i1 – i6) generally

switching from increasing to decreasing (Table 2, second entry). Intervals increased from 327.2 ± 32.5 msec (1st) to 356.5 ± 26.4 msec (3rd), and then decreased from 347.3 ± 28.9 msec (4th) to 329.0 msec (5th). The final interval increased slightly to 335.0 msec and these last two intervals are suspect due to small sample size.

Mode and mean number of beats per interspersed complex-female answer signals were 2 and 1.9 ± 0.9 msec (Table 1, second entry). Average interbeat intervals increased throughout the answer and overall they were 123.4 ± 75.3 msec. In symphonies, the (♂-♀) exchange intervals were 623.1 ± 78.6 msec and the (♀-♂) exchange intervals were 508.4 ± 166.7 msec. The terminal male response signals were different from sequenced and grouped calls with a mode and mean beat count of 4 (3.8 ± 1.1) and interbeat intervals of 135.3 ± 78.2 msec. Mean intervals of the response increased from 96.3 ± 16.7 (1st) to 299.3 ± 26.4 msec (5th). These data for complex-exchanges are compatible with all previous descriptions of this complex form of drumming. Only the elucidation of a changing interval description and ♂ (call) - ♂ (response) pattern are new information for this species.

One *I. zionensis* female answered male calls with a signal type other than tapping her abdomen. She fluttered her wings and her abdomen vibrated against the substrate for periods ranging from 2035.0 – 5352.9 msec. This wing-flutter behavior occurred after the male called from 1 to three times and often overlapped the male's next call.

Two recording sessions of this species took place during the morning when room temperature remained at 66º F (18.9º C). The two experimental pairs appeared to drum normally until analysis indicated a substantial difference in overall average call interval.

One hundred thirty-eight signals were obtained from two 3-4 day old males and two females respectively, under normal room lighting in Pitkin, Colorado. Their signal types ranged from 3-way sequences to long grouped exchanges, some as long as 5-way exchanges.

The male sequenced calls and grouped exchanges consisted of four mode beats (4.2 ± 0.5) with overall average intervals of 589.2 ± 50.7 msec (Table 3). The number of call groups ranged from 1-3, with individual mean interbeat call intervals (i1 – i4) increasing irregularly (Table 4).

Mode and mean number of beats per female answer signals were 2 and 2.3 ± 1.1 msec (Table 3). Overall average interbeat intervals were 206.7 ± 54.9 msec and the male response intervals averaged 184.7 ± 37.9 msec.

Isogenoides zionensis male and female sequenced and grouped exchanges at two temperatures (21–22°C and 18.9°C) had similar mode number of call- and answer-beats (Table 1 and Table 3), but overall beat intervals were larger for calls, answers and responses of colder males and females (Table 1 and Table 3), as would be predicted for poikilotherms.

Discussion

The overall summary of signal characters (Tables 1, 3) shows that when all parameters of male calls, female answers and duetting characteristics are considered, that *Isogenoides* drumming is species-specific. There is some overlap of beat intervals in two pairs: (1) *I. colubrinus* and *I. frontalis,* (2) *I. hansoni* and *I. varians*. This might be expected in this pair because of their morphological closeness, the fact that they were previously considered a single species (Hanson 1943) or subspecies (Ricker 1952), and

that their ranges have little overlap (except in Saskatchewan). The largely allopatric populations possibly have not been under selective pressure to diverge the beat interval parameter of their signals. The two *I. varians* populations appeared different in average beat intervals, possibly explained as geographically determined dialects. Although the average beat intervals of *I. hansoni* and *I. varians* show some overlap, there may be specificity in the actual change of intervals during calls. Those of *I. hansoni* decrease, while those of *I. varians* show slight increase. Additionally, when comparing the average call beat-count per group, *I. hansoni* is slightly larger (9.3 ± 4.3) than *I. varians* (6.5 ± 1.6). Further testing is necessary in order to confirm that beat-counts and actual intervals contain species-specific information recognized by these females.

Isogenoides drumming signals ranged from sequenced 2- to 3-way ♂ (call) - ♀ (answer) or ♂ (call) - ♀ (answer) - ♂ (response) exchanges to grouped male calls with grouped, interspersed female answers, terminated with or without a male response. One species, *I. zionensis* also had complex exchanges that may be described as containing long series of grouped or sequenced, or both grouped and sequenced exchange types. Pair-forming drumming characteristics and polarity of male-female exchange patterns (sequenced or non-multigrouped vs. grouped or multigrouped) were analyzed among six other drumming characters using an out group comparison (Watrous and Wheeler 1981) by Maketon and Stewart (1988). They determined that beat grouping was a strong derived character and that sequenced exchanges were ancestral by application of the “commonality principal” among all Arctoperlarian families (In-group “common = primitive”) (Watrous and Wheeler 1981).

Therefore, drumming in *Isogenoides* can generally be characterized as derived to varying degrees in all species, except *I. olivaceus*, since their calls, male-female exchange patterns and female answers contain predominately-sequenced signals. *Isogenoides olivaceus* exchanges were almost entirely ancestrally sequenced (N=269) with only one grouped exchange recorded in an eleven-day drumming period.

In general, *Isogenoides* male-female exchange patterns contain ancestral (sequenced exchanges) and derived (grouped exchanges) elements. Only *I. olivaceus* exchanges were the least specialized, almost entirely ancestrally sequenced (N= 269) with one grouped exchange recorded in an eleven-day drumming period.

Male-female exchanges with both sequenced signals and grouped exchanges exhibit intermediate specialization in complexity. This exchange type includes *I. colubrinus, I. elongatus, I. frontalis,* and *I. varians*.

The calls, male-female exchanges and answers of four species: *I. colubrinus*, *I. elongatus*, *I. frontalis*, and *I. varians*, contained both sequenced (ancestral) and grouped (derived) elements, and therefore appear to represent an intermediate transition in evolution of signaling (Stewart 2001) within the genus. The calls of *I. hansoni* (females were not successfully recorded) and calls, male-female exchanges and answers of both populations of *I. doratus* were exclusively grouped, and may therefore be considered derived and further specialized. The complex *I. zionensis* symphonies represent a third pattern of specialization, having both the sequenced ancestral and grouped elements for both sexes, and addition of two unique characters: 1. Grouped portion containing a switching interval pattern, and 2. The inclusion of a male terminal response signal immediately preceding a continuing call group (Fig. 8). The drumming of all

Isogenoides species fits at some level of the Stewart (2001) evolutionary paradigm, and the discussion of evolution of drumming in Perlodidae by Maketon and Stewart (1988).

Table 1. Drumming descriptions and signal characters for eight *Isogenoides* species. Numbers of signals and individuals, numbers of beats per group, and overall beat intervals are provided for male calls, female answers, and male responses.

Species (Location Code)	No. Signals / No. Individuals ♂	♀	♂	Range (Mode) Beats / Group $\bar{x}$ ± SD Beats / Group ♂	♀	♂	Overall Beat Intervals (msec) ($\bar{x}$ ± SD) ♂	♀	♂	Overall Exchange Intervals (msec) ($\bar{x}$ ± SD) ♂–♀	♀–♂	Last ♀–♂
I. colubrinus	115	114	113	3–7 (5)	1–4 (1)	1–6 (2)	65.0 ± 8.3	121.8 ± 26.8	441.8 ± 142.5	402.0 ± 101.2	1654.8 ±429.1	626.4 ± 198.5
(1) 5♂ 4♀	5	4	5	5.2 ± 0.7	1.8 ± 0.8	2.5 ± 0.9						
I. doratus	126	126		1–5 (3)	1–5 (2)		16.7 ± 3.0	107.0 ± 52.0		466.4 ± 89.4	699.4 ± 170.0	
(2) 1♂ 1♀	1	1		3.1 ± 0.6	2.1 ± 1.0							
(3) 4♂ 6♀	115	115		1–8 (3)	1–6 (1)		14.4 ± 3.8	135.5 ± 40.7		358.7 ± 79.9	724.8 ± 169.2	
	4	6		3.1 ± 1.2	1.5 ± 0.7							
I. elongatus	160	160	49	3–10 (7)	1–3 (3)	1–2 (1)	397.0 ± 75.0	386.9 ± 93.7	760.8 ± 222.7	925.5 ± 286.0	1971.9 ± 159.8	888.8 ± 294.8
(4) 7♂ 3♀	7	3	5	6.8 ± 1.1	2.5 ± 0.6	1.1 ± 0.3						
(5) 4♂ 3♀	121	120	57	4–8 (6)	1–3 (2)	1	222.1 ± 14.0	180.5 ± 20.7	N/A	570.0 ± 82.1	950.2 ± 124.1	648.3 ± 178.6
	4	3	4	5.9 ± 0.7	1.8 ± 0.5	1.0 ± 0.0						
I. frontalis[1]	135	135	132	2–6 (4)	1–3 (2)	1–8 (3)	61.2 ± 11.3	93.8 ± 29.3	288.8 ± 129.4	581.5 ± 76.3	1133.3 ± 307.2	427.7 ± 147.4
(6) 7♂ 1♀, (7) 1♀, (8) 3♂ 2♀	10	4	10	4.1 ± 0.7	1.6 ± 0.6	3.5 ± 1.6						
I. hansoni	60			5–19 (6)			31.3 ± 9.4					
(9) 4♂	4			9.3 ± 4.3								
I. olivaceus	269	243	88	5–8 (7)	1–10 (6)	1–6 (1)	98.2 ± 12.0	86.6 ± 22.0	356.5 ± 144.1	739.9 ± 130.9	831.6 ± 231.1	
(10) 2♂ 1♀, (11) 6♀	2	7	2	6.7 ± 0.5	5.5 ± 1.7	1.9 ± 1.0						
I. varians	125	115	58	2–10 (6)	1–5 (4)	1–7 (3)	26.7 ± 3.1	52.4 ± 9.2	56.0 ± 11.8	944.8 ± 64.0	1285.7 ± 276.3	892.8 ± 200.1
(12) 4♂ 5♀	4	4	4	6.5 ± 1.6	3.4 ± 1.0	3.2 ± 1.3						
(13) 4♂ 2♀	117	100	38	2–11 (8)	1–5 (2)	1–5 (3)	36.9 ± 4.0	56.7 ± 9.7	73.4 ± 21.4	839.9 ± 61.4	1279.4 ± 305.2	919.4 ± 113.5
	4	2	4	7.1 ± 1.5	2.4 ± 0.9	3.1 ± 0.9						
I. zionensis	307	307	299	1–6 (4)	1–7 (2)	1–6 (3)	364.3 ± 59.1	136.8 ± 32.7	132.2 ± 43.4	624.3 ± 129.3	561.2 ± 197.3	534.9 ± 147.8
(14) 7♂ 9♀	7	9	7	4.0 ± 0.6	2.2 ± 1.1	3.7 ± 1.4						
(14) 2♂ 5♀	21	21	39	1–6 (4)	1–4 (2)	2–6 (4)	344.8 ± 32.2	123.4 ± 75.3	135.3 ± 78.2	623.1 ± 78.6	508.4 ± 166.7	453.2 ± 175.9
	2	5	2	3.6 ± 1.1	1.9 ± 0.9	3.8 ± 1.1						

[1]. (Sandberg and Stewart 2003)

Table 2. Summary data for number of male call groups per exchange and individual average sequenced and/or grouped male call intervals (msec). Generalized average interval descriptions described as increasing (I), decreasing (D) and switching (S), are indicated at the ends of sequenced and/or grouped data. (I-D) increasing then decreasing defines the switching intervals.

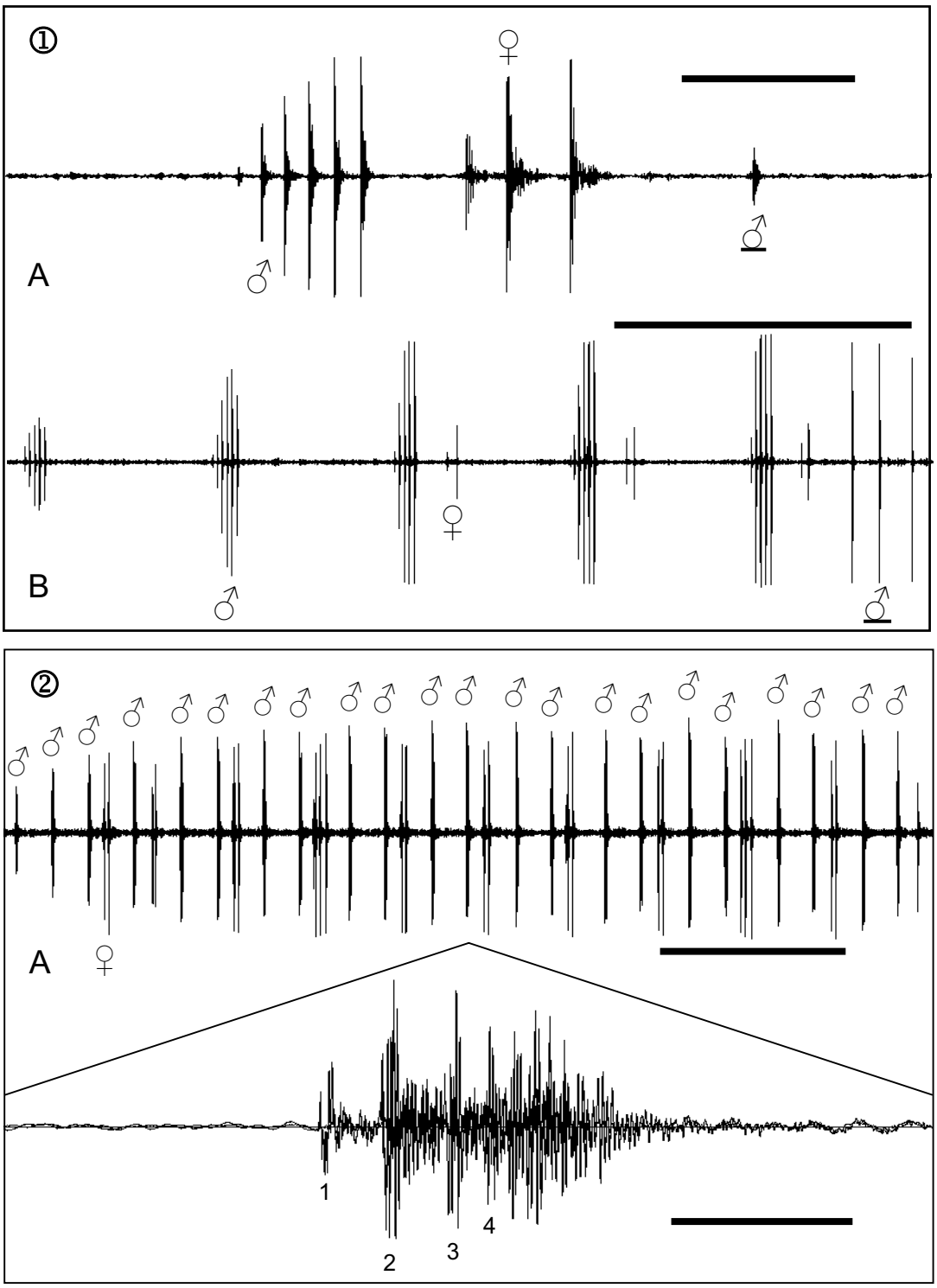
Species (Location Code)	# Call Groups Range (Mode) $\bar{x}$ ± SD	Summarized ♂ Average Call Intervals / Group																	
		i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	i17	i18
I. colubrinus	1–7 (2)						N=10												
(1) 5♂ 4♀	3.0 ± 1.4	59.7	63.1	66.2	69.2	72.6	69.4	**I**											
I. doratus	2-21 (11)				N=9														
(2) 1♂ 1♀	9.7 ± 4.0	17.5	17.4	10.1	12.4	**D**													
	2-22 (6)							N=1											
(3) 4♂ 6♀	6.5 ± 2.9	16.7	15.2	9.2	6.9	6.8	6.5	7.7	**D**										
I. elongatus	1-3 (1)									N=2									
(4) 7♂ 3♀	1.1 ± 0.3	354.4	386.4	398.4	403.0	407.8	427.5	442.8	472.5	638.3	**I**								
	1-3 (1)																		
(5) 4♂ 3♀	1.2 ± 0.4	207.5	219.9	225.9	229.2	228.0	230.3	242.1	**I**										
I. frontalis	1-6 (3)					N=1													
(6) 7♂ 1♀, (7) 1♀, (8) 3♂ 2♀	3.2 ± 1.3	51.9	59.2	68.7	77.3	65.5	**I**												
Isogenoides hansoni	3																		N=4
(9) 4♂		35.0	34.6	32.6	32.0	29.9	29.0	29.2	30.1	29.7	30.0	29.4	28.8	28.6	28.6	28.2	27.3	25.0	25.6 **D**
I. olivaceus	1-3 (1)																		
(10) 2♂ 1♀, (11) 6 ♀	N/A	107.0	105.9	102.4	95.1	89.8	86.1	85.8	**D**										
Isogenoides varians	1-7 (3)								N=33	N=5									
(12) 4♂ 5♀	3.4 ± 1.3	25.8	26.3	26.4	26.9	27.3	28.0	28.0	27.1	30.0	**I**								
	1-6 (3)								N=42	N=5	N=2								
(13) 4♂ 2♀	3.4 ± 1.3	35.4	35.6	36.0	37.0	37.7	38.6	39.2	41.7	40.2	44.4	**I**							
I. zionensis	1-3 (1)				N=59	N=1													
(14) 7♂ 9♀	1.2 ± 0.4	337.6	377.5	380.3	359.8	344.4	**S**	**(I-D)**											
	2-6 (2)				N=5	N=1	N=1												
(14) 4♂ 5♀	2.9 ± 1.1	327.2	353.6	356.5	347.3	329.0	335.0	**S**	**(I-D)**										

Table 3. Drumming description and characters for *I. zionensis* at the colder 66º F (18.9º C). Numbers of signals and individuals, numbers of beats per group, and overall beat intervals are provided for male calls, female answers, and male responses.

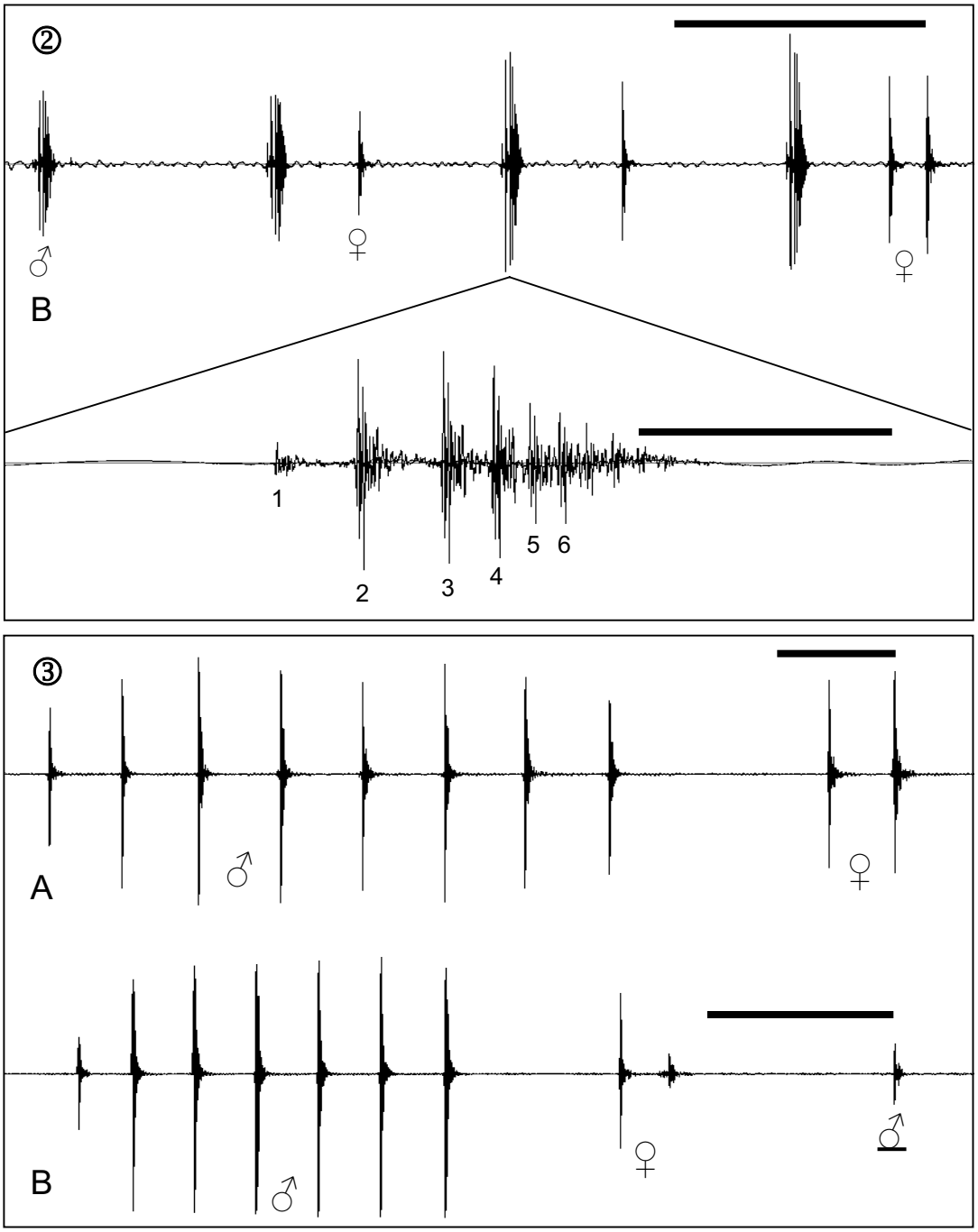
Species (Location Code)	No. Signals / No. Individuals ♂	♀	♂	Range (Mode) Beats / Group $\bar{x}$ ± SD Beats / Group ♂	♀	♂	Overall Beat Intervals (msec) ($\bar{x}$ ± SD) ♂	♀	♂	Overall Exchange Intervals (msec) ($\bar{x}$ ± SD) ♂–♀ (♂–♂)	♀–♂	Last ♀–♂
I. zionensis	138	115	124	2–5 (4)	1–5 (2)	1–6 (3)	589.2 ± 50.7	206.7 ± 54.9	184.7 ± 37.9	2015.1±101.2	1327.0±171.3	921.2 ± 321.8
(14) 2♂ 2♀	2	2	2	4.2 ± 0.5	2.3 ± 1.1	3.7 ± 1.1						
(66º F)												

Table 4. Summary data for number of male call groups per exchange and individual average sequenced and/or grouped male call intervals (msec). Generalized interval descriptions described as increasing (I) are indicated at the end of sequenced and/or grouped data. First substantial interval increase is indicated with a shaded box.

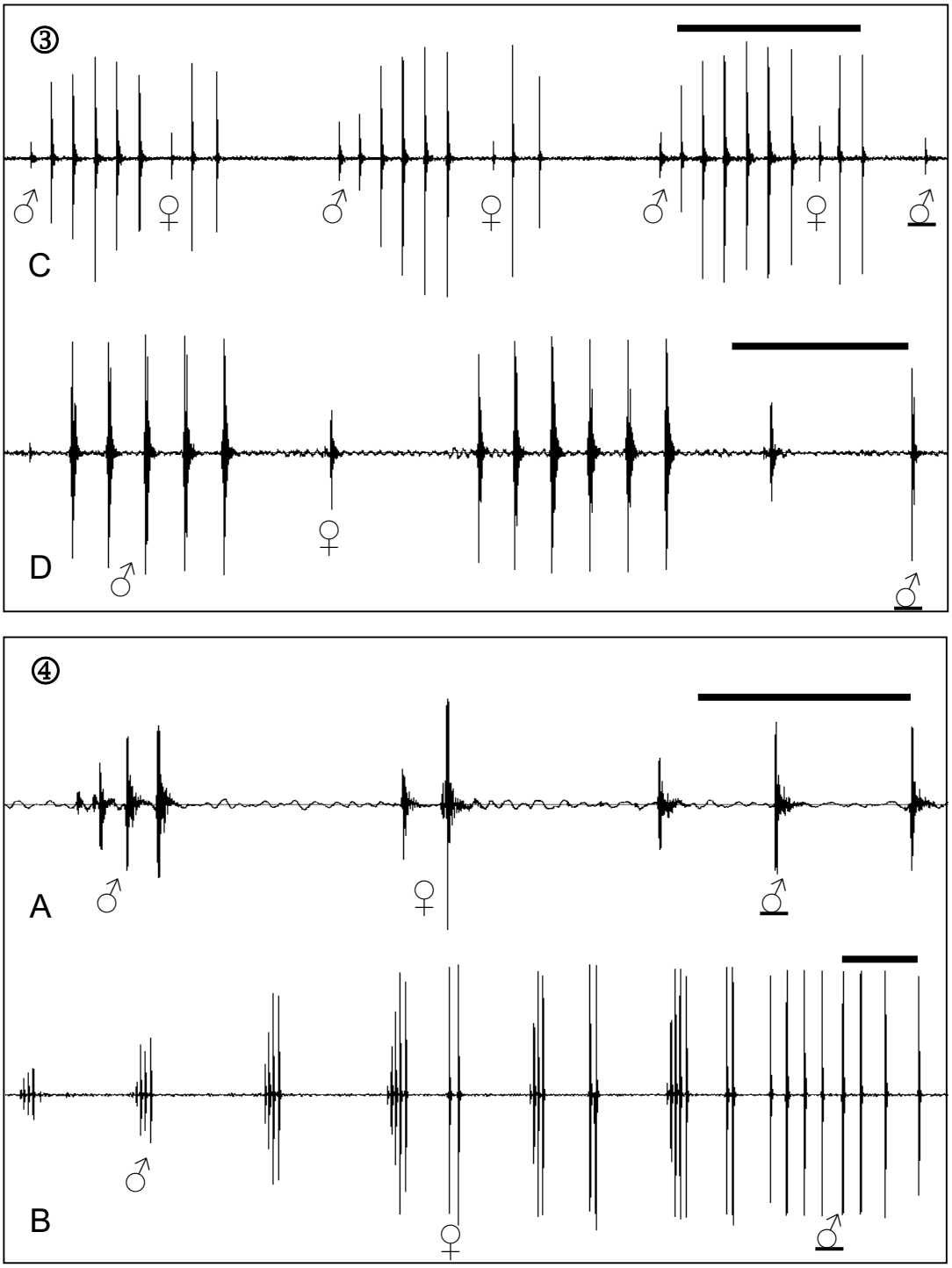
Species (Location Code)	Call Groups Range (Mode) $\bar{x}$ ± SD	Summarized Average Beat Intervals / Group i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	i17	i18
I. zionensis	1–3 (1)				N=35														
(14) 2♂ 2♀	1.3 ± 0.6	549.1	604.7	609.1	617.5	I													
(66º F)																			



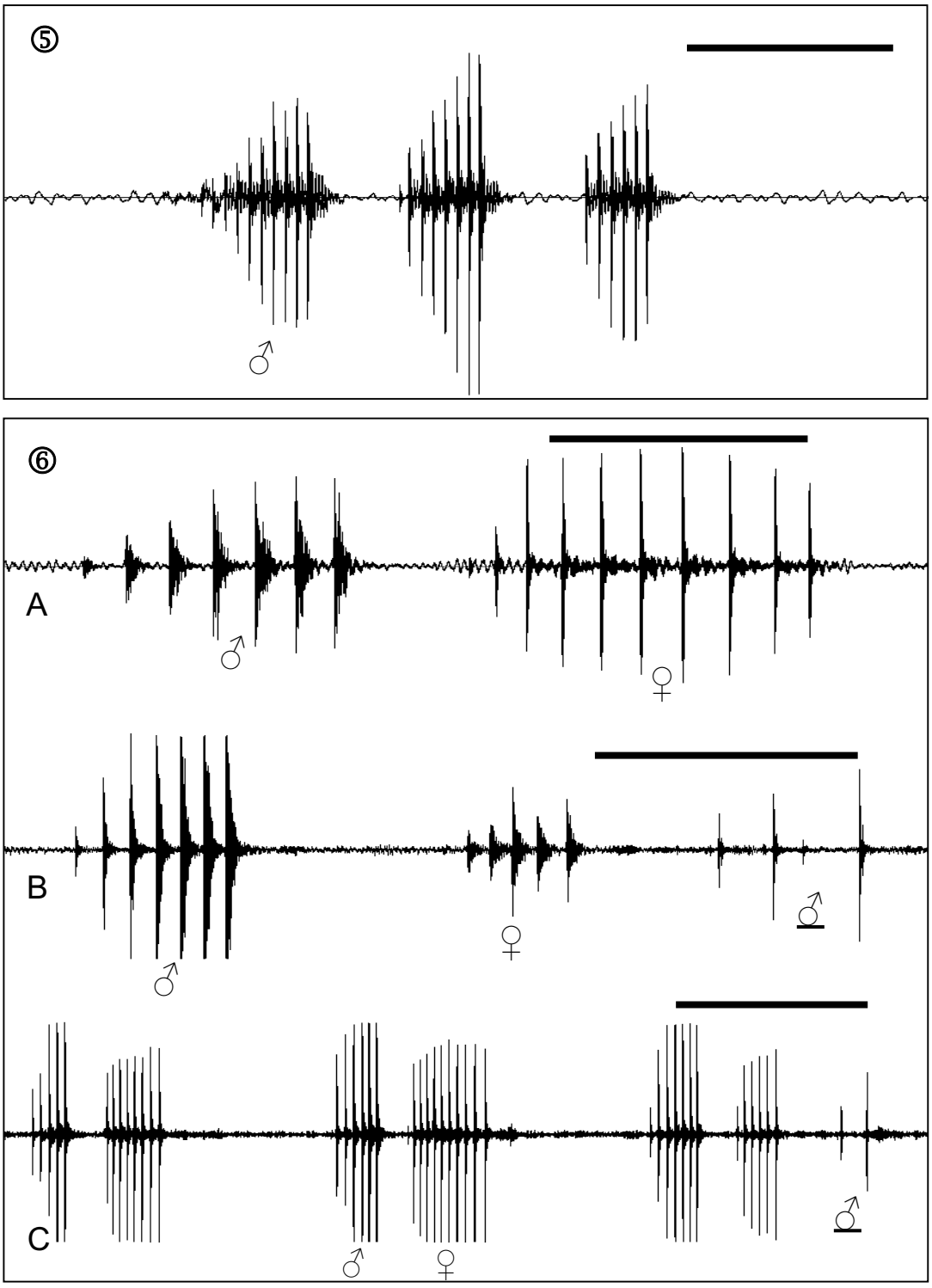
Figures 1–2. 1. *Isogenoides colubrinus* drumming. (A) Call-answer-response, 3-way sequence, Bar = 500 msec; (B) Grouped exchange. Bar = 5000 msec. 2. *Isogenoides doratus* drumming. (A) Michigan Grouped exchange, Bar = 5000 ms, Total duration 24,288 msec. Dropdown: 100X horizontal zoom of male call group 12, Bar = 50 msec.



Figures 2–3. 2. *Isogenoides doratus* drumming. (B) Iowa Grouped exchange, Bar = 1000 msec. Dropdown: 20X horizontal zoom of male call group 3, Bar = 50 msec. 3. *Isogenoides elongatus* drumming. (A) 1999 Granby, CO, Sequenced call-answer, Bar = 500 msec. (B) 1999 Granby, CO, Call-answer-response, 3-way sequence, Bar = 1000 msec.



Figures 3–4. 3 (C) *Isogenoides elongatus* drumming. 1999 Granby, CO, 7-way grouped exchange, Bar = 3000 msec. (D) 2000, Rifle, CO, 5-way grouped exchange, Bar = 1000 msec. 4. *Isogenoides frontalis* drumming. (A) Call-answer-response, 3-way sequence, Bar = 500 msec. (B) Grouped exchange, Bar = 1000 msec.



Figures 5–6. 5. *Isogenoides hansoni* drumming. Male grouped calls, Bar = 500 msec. 6. *Isogenoides olivaceus* drumming. (A) Sequenced call-answer, Bar = 1000 msec. (B) Sequenced 3-way call-answer-response, Bar = 1000 msec. (C) Grouped 7-way exchange, Bar = 2000 msec.

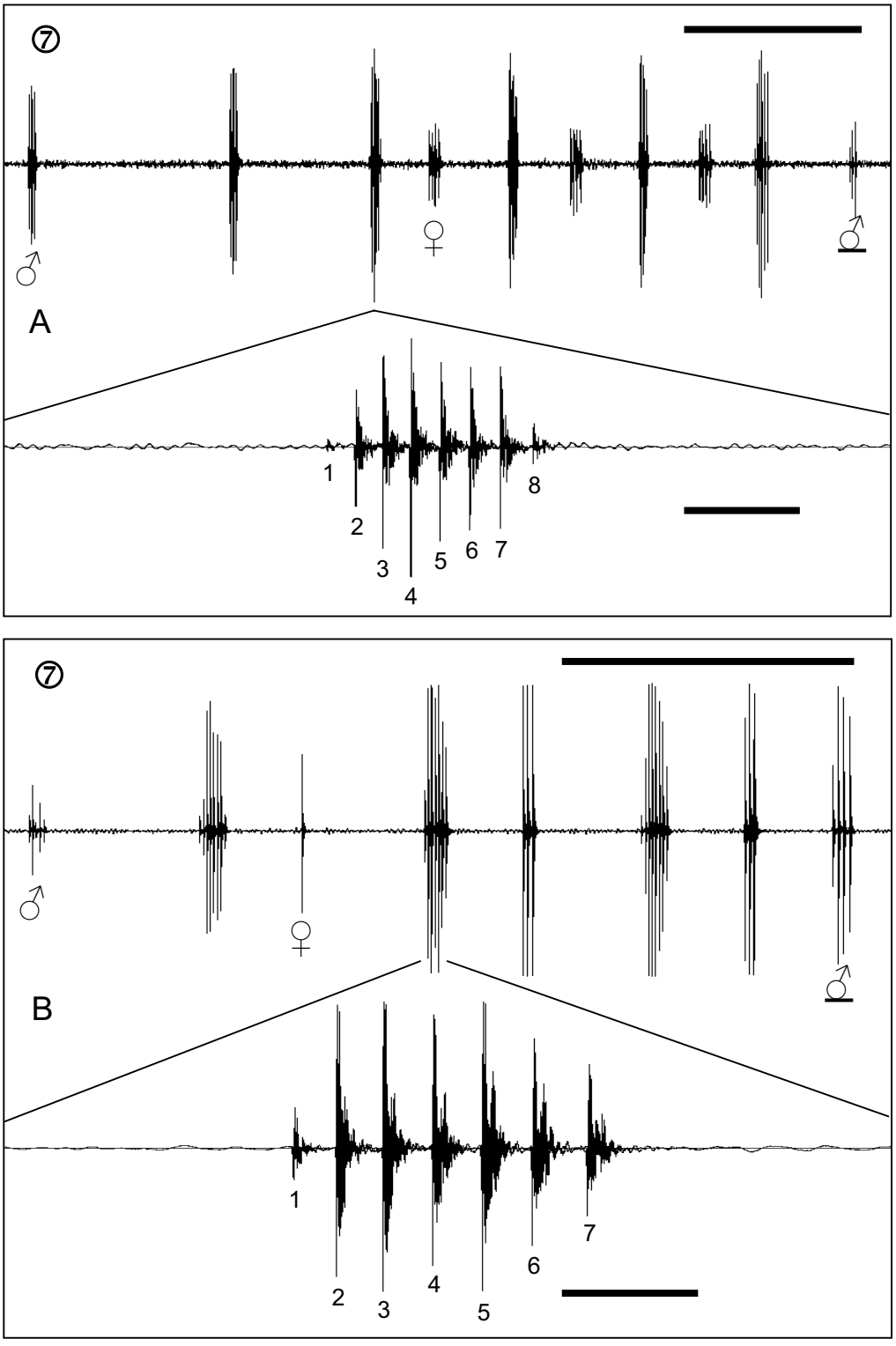


Figure 7. *Isogenoides varians* drumming. (A) 2000 Mississippi, grouped exchange, Bar = 3000 msec., Dropdown: 20X horizontal zoom of male call group 3, Bar = 100 msec. (B) 2001 Virginia, grouped exchange, Bar = 3000 msec., Dropdown: 15X horizontal zoom of male call group 3, Bar = 100 msec.

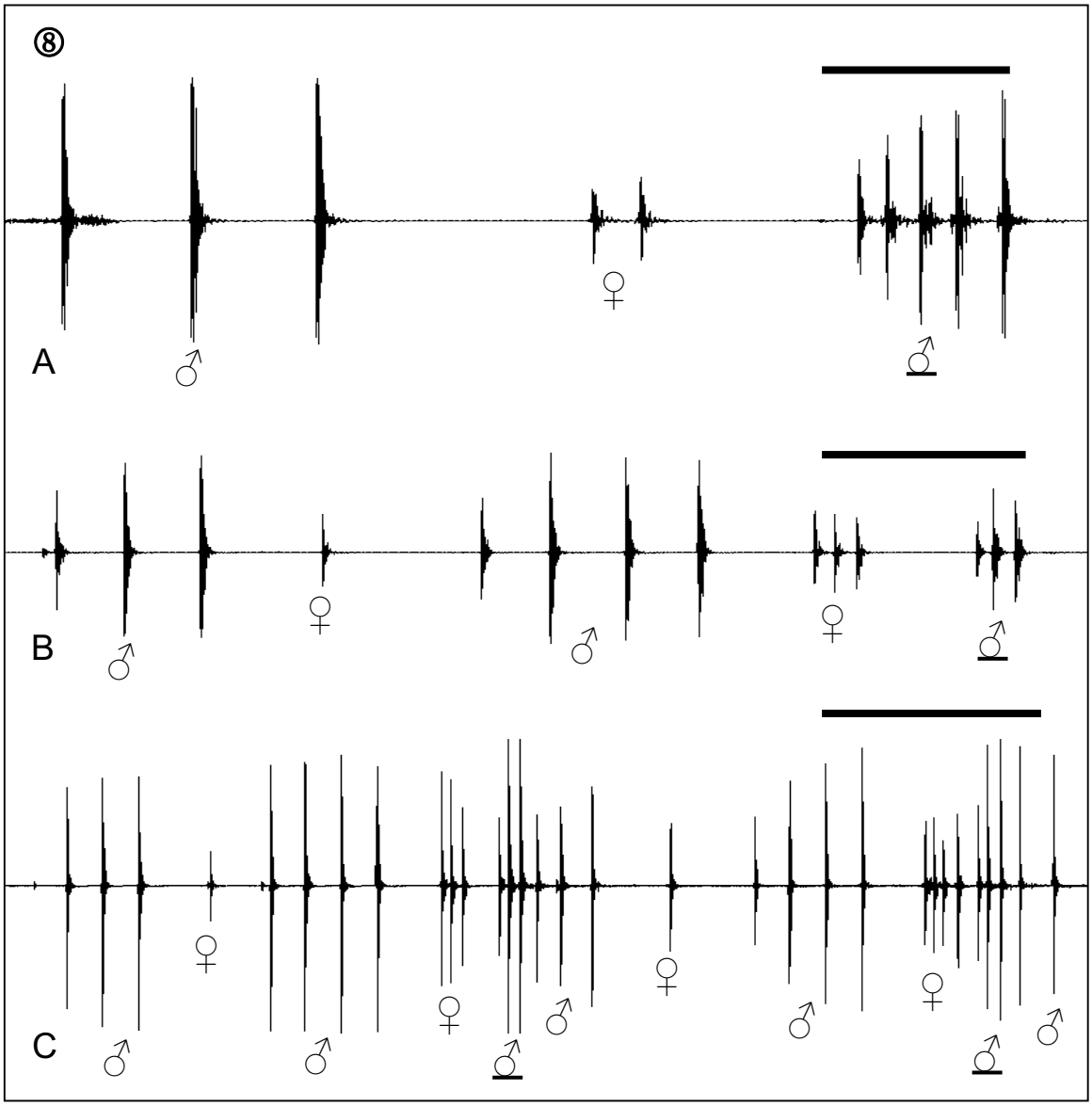


Figure 8. *Isogenoides zionensis* drumming. (A) Call-answer-response, 3-way sequence, Bar = 500 msec. (B) Grouped exchange, Bar = 1000 msec. (C) Complex grouped exchange, Bar = 2000 msec.

CHAPTER 4

CAPACITY FOR EXTENDED EGG DIAPAUSE IN SIX *Isogenoides* KLAPÁLEK SPECIES (PLECOPTERA: PERLODIDAE)

Introduction

The eggs of some homodynamic stonefly species hatch directly within a few weeks after oviposition (Harper 1973, Hynes 1976, Stewart and Stark 2002, Zwick and Hohmann 2003), or may extend or delay development and hatching over short or long number of days by dormancy, depending on temperature experienced during incubation (Brittain 1977, Lillehammer 1986, 1987, Elliott 1989, Frutiger 1996, Zwick 1996a, b, 2002, Stewart and Stark 2002). Eggs of the few heterodynamic species that have been studied have the capacity for extended, and sometimes asynchronous diapause with hatching from 5–7 months up to three years or possibly longer (Khoo 1968a, Marten 1991, Oberndorfer and Stewart 1977, Snellen and Stewart 1979a, b). The strategies of dormancy or diapause allow “waves of hatch” (Hynes 1976), cohort splitting (Butler 1984, Humpesch and Elliott 2003) or asynchronous hatch over several years, sometimes missing a season or even year(s). Such extended egg development is presumably an adaptation, probably genetically programmed, to enhance survival through unpredictable or adverse temperatures, water flow or other environmental conditions. Either dormancy or diapause of eggs may be in different phases of development (with no apparent eyespot appearance) or as an arrested development of protonymphs within the egg (apparent eyespot appearance), but this has not been delineated in most previous studies.

The strategy of sibling eggs from a single batch or female, or seasonal adult population, breaking diapause and hatching at different times, results in nymph recruitment over extended periods. This enhances the probability of favorable conditions for survival of at least some of the progeny, fulfilling at least in part the presence of r–adaptiveness in insects that produce large numbers of eggs. Zwick (1996a, 2002) has proposed that dormant or diapausing eggs in streams represent a "seed bank" from which recruitment of nymphs may be made over an extended time. Giesel (1976) used the phrase "relict seeds" for eggs with delayed and sometimes asynchronous development that allows parents to effectively prolong their reproductive life span. Humpesch and Elliott (1987, 2003) proposed that delayed egg development with a long hatching period is one mechanism for life cycle partitioning and enhanced nymph survival in Plecoptera and Ephemeroptera.

Our knowledge of stonefly egg development must still be considered meager from the standpoint of the few detailed experimental incubation studies that represent few genera and species in the families Chloroperlidae (Lillehammer 1987, Harper 1973), Leuctridae (Lillehammer 1985, Elliott 1987, Snellen and Stewart 1979a), Nemouridae (Elliott 1986, Brittain and Lillehammer 1987, Harper 1973), Perlidae (Elliott 1991a, Harper 1973, Snellen and Stewart 1979b, Lillehammer 1986, 1987, Marten 1991, Frutiger 1996, Moreira and Peckarsky 1994, Zwick 1996a, b, 2002), Perlodidae (Khoo 1968a, Harper 1973, Oberndorfer and Stewart 1977, Elliott 1991b, DeWalt and Stewart 1995, Sandberg and Szczytko 1997) and Taeniopterygidae (Khoo 1968b, Brittain 1977, Zwick and Hohmann 2003).

The North American stonefly genus *Isogenoides* currently contains 9 species. The eggs of all except *I. colubrinus*, *I. elongatus* and *I. zionensis* were studied and figured with SEM by Kondratieff (2004), who found no distinguishing differences in species. Egg development and hatching are unknown except for the Dewalt and Stewart (1995) study establishing that the eggs of *I. zionensis* from the Rio Conejos of Colorado diapaused at least over their first summer and winter. Eggs laid by June-emerging females hatched in March–April the following year. This, and the study by Oberndorfer and Stewart (1977), proving that eggs of the perlodid *Hydroperla crosbyi* in Texas undergo diapause for approximately eight months, from February-emerging females until about October, led us to be interested in determining the prevalence of diapause in the genus *Isogenoides*, and the capacity of eggs of various species for extended and asynchronous diapause. Our study of the systematics and drumming of *Isogenoides* (unpublished), that began in 1999, afforded the opportunity to collect and rear nymphs, mate virgin adults, and obtain eggs for incubation experiments to address these questions for six species.

Materials and Methods

Species and Collection Sites

This study was begun in 1999, and still in progress in fall 2004, with eggs of the various species and populations having been in incubation from approximately 1.5 to 5 years. Virgin adults of six species were reared from mature nymphs collected as follows: (1) *I. colubrinus* (Hagen), Yampa River at 12 Mile Gulch and Cross Canyon, 7.1 miles NW of Elk Springs, Moffat Co., Colorado, 28 May 2000; (2) *I. doratus* (Frison), Rock River at Lakewood Corner on Hwy 75, 7 miles South of Rock Rapids,

Lyon Co., Iowa, 09 February 2002; (3) *I. elongatus* (Hagen), Colorado River at Riffle city park, Garfield Co., Colorado, 12 March 2000; (4) *I. frontalis* (Newman), Rocky Run Creek, 1.5 miles North of Brule, Douglas Co., Wisconsin, 07 April 2000; (5) *I. frontalis* (Newman), Confluence of Fish and Pine Rivers, Intersection of Fish Cr. Rd. and Old US 2, Bayfield Co., Wisconsin, 09 April 2000; (6) *I. varians* (Walsh), Big Otter River, Bridge on Hwy 24 @ CR 711 and 709 intersections, 2 miles West of Campbell County line, Bedford Co., Virginia, 26 February 2001; (7) *I. zionensis* Hanson, San Miguel River @ Placerville, San Miguel Co., Colorado, June 1999; (8) *I. zionensis*, San Miguel River @ Specie Cr., 5 miles West of Placerville, San Miguel Co., 14 June 2000; (9) *I. zionensis*, Leopard Creek, Hwy 62, 4 miles North of Placerville, San Miguel Co., 29 June 2000.

Rearing

Pre-emergent nymphs from field collections were held and reared individually in perforated foam cups containing stream substrate, suspended in a Living Stream® controlled environment (Frigid Units Inc.®, Toledo, OH, http://www.frigidunits.com/). The laboratory stream was adjusted to a single simulated seasonal temperature regime determined by submerging a Ryan® temperature monitor Model RL100™ (Ryan® Instruments, Redmond, WA, http://www.ryaninst.com/) in the San Miguel River, Colorado, for the period July 1999 to July 2000. During that year, the laboratory stream was adjusted to periodic San Miguel River temperatures obtained from a mercury thermometer during trips from Texas to Colorado for an associated study of *I. zionensis* life history (Fig. 1). In subsequent years, the Living Stream® temperature regime was kept as close as possible to the simulated annual regime, read from the Ryan® temperature charts, with some usually minor fluctuations due to functional variations of

the Living Stream® temperature regulator (Fig. 1). Photoperiod was adjusted from a minimum of 9.5 hr of fluorescent room light (January 1–15) to a maximum of 14.5 hr (June).

Emergent adults were transferred to individual foam cups and labeled with species, sex and emergence date. They were paired beginning after 1–7 days, and allowed to mate by transferring a male into the female's container.

Collection and Incubation of Eggs

When an egg mass was produced by a mated female, it was placed in stream water in a small, approximately 8 ml glass container, covered with 100 μm mesh plastic bolting cloth, labeled by date and female, kept in larger glass container, and incubated in the laboratory stream at its annual temperature regimes (Fig. 1) for the duration of the study.

Fungal growth inside incubation containers was controlled in 2000 and 2001 using stabilized chlorine oxides in the commercial tropical aquarium MarOxy® anti-fungal solution (Mardel Laboratories, Inc., Harbor City, CA, http://www.mardel-labs.com/) and an aqueous solution of Methylene Blue. These treatments were added to egg incubation containers monthly, during these years, when large amounts fungal hyphae were observed. After 2001, no more treatments were needed.

Egg Inspection and Recording of Hatch

Incubation containers were visually inspected, usually weekly over the long period, for hatch by removing them from the larger containers, and gently shaking them while looking for movement or suspension of hatchlings. If presence of young larvae

was detected, then that container was opened and its contents scanned under a dissecting microscope at 0.8–50X. A 2.5 cc syringe was used to siphon up the live or dead hatchlings and any exuviae, their numbers recorded, and remaining eggs were returned to the large glass containers containing stream water, and to the laboratory stream within 0.5–3.0 hr. to ameliorate as much as possible any thermal stress. Each incubation container was emptied into a petri dish for removal of dead eggs and post-hatch eggshells at approximate 6-month intervals. Dead or damaged eggs were black or clear inside. Only eggs that were near hatching had eyespots of the developing protonymph visible inside the chorion. These, and eggs with solid white contents, whether or not covered with fungus or algae, were considered viable and were returned to the laboratory stream within 0.5–3.0 hr. First instars, older hatchlings and exuviae were counted and preserved in 80% ethyl alcohol (EtOH) and held in genitalia vials in larger 4-dram vials labeled by date, egg batch and female origin. Final totals of eggs/mass were determined from accumulated counts over the variable incubation period for each species.

Results

Viable eggs from all six *Isogenoides* species were successfully obtained and incubated, with an overall 24–92% hatch over the variable periods of approximately 14 days to 4 years (Table 1).

Isogenoides colubrinus Four egg masses from each of four females were placed into the laboratory stream environment between 03–18 June 2000, when simulated regime temperature ranged from 12–17ºC (Fig. 1). Hatch was not direct in the year of deposition, and eggs diapaused approximately 10 months until some began

hatching in April 2001 (Fig. 2) when stream temperature was 10ºC, and they continued hatching until late June. The remaining eggs continued diapause through approximately 11 months (July 2001 to June 2002) of their second year. The last eggs to hatch from all female masses occurred between 12 June and 20 July 2002, when temperature was 13.5ºC. None hatched in 2003, and on 24 February 2004, the remaining 50 eggs had no eyespots but appeared to be viable. Through that date, then, a 37–79% hatch had been obtained for the four egg batches, with a confirmed asynchronous extended diapause and hatch extending over at least two years; average total number of eggs/batch was 632.5 (Table 1, Fig. 2).

Isogenoides doratus One egg mass from one female, containing 996 eggs, was placed into the laboratory stream environment on 16 April 2002, when simulated regime temperature was 6ºC (Fig. 1). Hatch was not direct, and eggs diapaused approximately 3–5 months over the summer, until 34% hatched between 03 August and 21 September 2002 (Fig. 3). On 24 February 2004, the remaining 616 eggs were examined under the dissection microscope; none had eyespots and they appeared to remain alive (Table 1). Through that date, then, only an over-summer diapause has been confirmed for this species.

Isogenoides elongatus Six egg masses from each of six females were placed into the laboratory stream environment between 01–11 May 2000, when simulated regime temperature was12ºC (Fig. 1). Hatch was not direct in the year of deposition and eggs diapaused approximately 11.5 months until some began hatching 14 April 2001, (Fig. 4) when stream temperature was 10ºC. Hatching continued until 30 June 2001. The remaining eggs continued diapause through approximately 11 additional

months until a small hatch resumed again in June 2002, and another very small hatch of six eggs occurred April–June 2003 (Fig. 4). On 24 February 2004, the remaining 425 eggs appeared to remain alive in incubation (Table 1), and six of these had eyespots suggesting further expected hatching with increasing temperature. Through that date, then, a 24–92% hatch had been obtained for the six egg batches, with a confirmed asynchronous egg diapause and hatch extending over at least three years; average total number of eggs/batch was 708.2 (Table 1, Fig. 4).

Isogenoides frontalis Six egg masses from each of six females were placed into the laboratory stream environment between 24–26 May 2000, when simulated regime temperature was12ºC (Fig. 1). Hatch was not direct in the year of deposition, and eggs diapaused through approximately 10.5 months until some began hatching on 14 April 2001, (Fig. 5) when stream temperature was 10ºC. Coincidentally, this is the same date that *I. elongatus* began to hatch. Hatching continued until 16 June 2001, and the remaining egg continued diapause though approximately 12 additional months until hatching resumed again in June and early July 2002. Another very small hatch of six eggs occurred April–June 2003, after approximately 10–12 additional months of diapause. On 24 February 2004, the remaining 210 eggs (Table 1) were examined under the dissection microscope; they appeared to remain alive and only one had eyespots. Through that date, then, a 33–88% hatch had been obtained for the six egg batches, with a confirmed asynchronous egg diapause and extended hatching over at least three years; average total eggs/batch was 415 (Table 1, Fig. 5).

Isogenoides varians One egg mass from one female, containing 94 eggs, was placed into the laboratory stream environment on 14 April 2001, when simulated

regime temperature was 6ºC (Fig. 1). Hatch was not direct, and eggs diapaused through approximately 4 months, over summer, until 92% of them hatched over a 13-day period from 18 August to 01 September, when stream temperature was 16ºC (Fig. 6). Another very small hatch of seven eggs began on 24 August 2002, after approximately 11.5 additional months of diapause and continued until 31 August. The remaining five eggs on 24 February 2004, (Table 1) were consumed by fungal infection and removed from the laboratory stream. Therefore, 92% of the 94 eggs hatched, with a confirmed asynchronous egg diapause and hatch extending over at least one year.

Isogenoides zionensis On 26 June, 1999, a single egg mass, containing 368 eggs, from one San Miguel River, Colorado, female was collected and temporarily held in Quartz Creek, Colorado, at temperatures ranging from 10–12ºC; and then later placed into the laboratory stream on 16 July, 1999, at 11ºC (Fig. 1). A second egg batch, containing 733 eggs, collected from a second San Miguel River female was placed into the laboratory stream on 14 June 2000, when stream temperature was 17ºC (Fig. 1). Two egg masses, containing 1092 eggs, from one Leopard Creek, Colorado, female were collected and placed in a single container on 01 and 06 June, 2000, when laboratory stream temperature was 12ºC (Fig. 1). These two masses have been treated as one in this study.

The Leopard Creek batches (squares in figure) began hatching directly on 14 June, 2000, when stream temperature was 17ºC, with the first 19 hatchlings only requiring from 8–14 days of development (Fig. 7). Hatching continued for 3 months and ended on 22 September, when stream temperature had decreased to 9ºC. The remaining eggs continued diapause until some began hatching on 10 March 2001, and

continued through late June; only one nymph emerged later on 1 September 2001 (Fig 7.). Over the three remaining two years and two months of development, only one egg hatched on 12 June 2002, none hatched in 2003, and two hatched early on 23 February, 2004, presumably because our laboratory stream malfunctioned and temperature increased to 15ºC for an unknown period of possibly 48 to 72 hours. On 24 February 2004, the remaining 404 eggs (Table 1) appeared to remain alive; three eggs had eyespots suggesting further expected hatching as temperature increases. Through that date, then, a 38% hatch had been obtained with a confirmed direct and asynchronous extended diapause and hatch over at least three years.

The 1999 San Miguel River batch (diamonds in figure) did not develop directly in the year of deposition, and began hatching on 6 March 2000, when stream temperature was 6ºC, after approximately eight months of diapause. Hatching continued until 05 July 2000. The remaining eggs continued diapause until some resumed hatching on 14 April and 12 May, 2001, when stream temperature was 10–11ºC. No additional hatching occurred, of the 13 eggs that have appeared to remain alive through 24 February, 2004; none had eyespots on that date. Through that date, then, a 36% hatch had been obtained with a confirmed asynchronous extended diapause and hatch extending over at least one year.

The 2000 San Miguel River egg mass (circles in figure) was deposited on 14 June 2000, and experienced a nine-month diapause until the first hatching on 11 March 2001, when stream temperature was 6ºC. Hatching continued until 23 June, when stream temperature was 12ºC. Over the remaining three years, 10 eggs hatched on 12 June 2002, 4 hatched on 26 April 2003, and 2 hatched on 23 February 2004,

presumably due to a temporary increase in the laboratory stream temperature. On 24 February 2004, 190 apparently live eggs remained and three had eyespots suggesting further expected hatching. Through that date, then, a 38% hatch had been obtained with a confirmed asynchronous diapause and hatch extended over at least four years.

Discussion

The results show a great capacity in the genus *Isogenoides* for extended, sometimes asynchronous, egg diapause and hatching, and that diapause in all species studied occurs early in development with no apparent eyespot appearance until just before hatching. The incubation of eggs of the six species populations from widely separated latitudes and longitudes of North America, at a single seasonal temperature regime, suggest that this capacity in each species is intrinsically, probably genetically, controlled. The simulated San Miguel River, Colorado, seasonal temperature regime yielded good cumulated 24–92% egg mass hatch percentages (Table 1) despite the fact that it probably did not closely correspond with the natural seasonal regimes of the origin streams of most tested populations, particularly of Iowa (*I. doratus*), Wisconsin (*I. frontalis*), or Virginia (*I. varians*). The declining and small hatches after one year of diapause (*I. colubrinus* Fig. 2, *I. elongatus* Fig. 4, *I. frontalis* Fig. 5) could be a reflection of the unnatural experimental temperature regime, other conditions not met in the laboratory stream, or an intrinsic, genetically programmed decline over extended years.

The number of presumably live eggs remaining for various species in February, 2004 (Table 1), leaves open the possibility of an additional year or more of extended hatch, beyond that recorded for some species. The study should be followed up by incubating eggs of each species at their origin-stream seasonal temperatures over

extend years, to more precisely determine the details of their diapause adaptation. An attempt was made in January-February, 2004, to obtain eggs for incubation, of the southernmost known population of *I. varians* of Westville Creek, in Simpson County, Mississippi. Three males and eight females were reared and paired, as described above for other species, but copulation was not observed and females extruded no egg masses.

Table 1. Emergence, mating, egg mass deposition dates, and numeric egg hatch summary data (February 2004) for six species of *Isogenoides*. Species ID are species initials except for *I. zionensis* where locations (San Miguel River and Leopard Creek) are indicated.

Species ID	Date Emerged	Date Mated	Date Deposition	Total # Masses/ # Eggs	# Eggs Hatched (% Hatch)	# Eggs Dead-Damaged	Remaining # Eggs Incubating
IC-01	02-VI-2000	02-VI-2000	03-VI-2000	1/801	566 (71)	227	8
IC-02	02-VI-2000	04-VI-2000	05-VI-2000	1/906	679 (75)	219	8
IC-03	11-VI-2000	11-VI-2000	12-VI-2000	1/572	453 (79)	107	12
IC-04	15-VI-2000	16-VI-2000	18-VI-2000	1/251	92 (37)	137	22
ID-01	09-IV-2002	13-IV-2002	16-IV-2002	1/996	340 (34)	40	616
IE-01	01-VI-2000	01-VI-2000	01-VI-2000	1/531	306 (58)	177	48
IE-02	04-VI-2000	04-VI-2000	05-VI-2000	1/436	104 (24)	309	23
IE-03	06-VI-2000	06-VI-2000	06-VI-2000	1/859	444 (52)	242	173
IE-04	07-VI-2000	07-VI-2000	07-VI-2000	1/967	629 (65)	318	20
IE-05	11-VI-2000	11-VI-2000	11-VI-2000	1/848	558 (65)	132	158
IE-06	11-VI-2000	11-VI-2000	11-VI-2000	1/608	558 (92)	47	3
IF-01	22-V-2000	23-V-2000	24-V-2000	1/532	184 (35)	283	65
IF-02	24-V-2000	24-V-2000	24-V-2000	1/614	202 (33)	404	8
IF-03	22-V-2000	23-V-2000	24-V-2000	1/395	325 (82)	25	45
IF-04	23-V-2000	24-V-2000	26-V-2000	1/364	322 (88)	25	17
IF-05	21-V-2000	25-V-2000	26-V-2000	1/383	307 (80)	25	51
IF-06	25-V-2000	25-V-2000	26-V-2000	1/200	95 (47)	81	24
IV-01	05-IV-2001	12-IV-2001	14-IV-2001	1/94	86 (92)	8	0
SMR-01	24-VI-1999	25-VI-1999	26-VI-1999	1/368	134 (36)	221	13
SMR-02	02-VI-2000	14-VI-2000	14-VI-2000	1/733	283 (38)	260	190
LC-01	29-V-2000	31-V-2000	1 & 6-VI-2000	2/1092	419 (38)	269	404

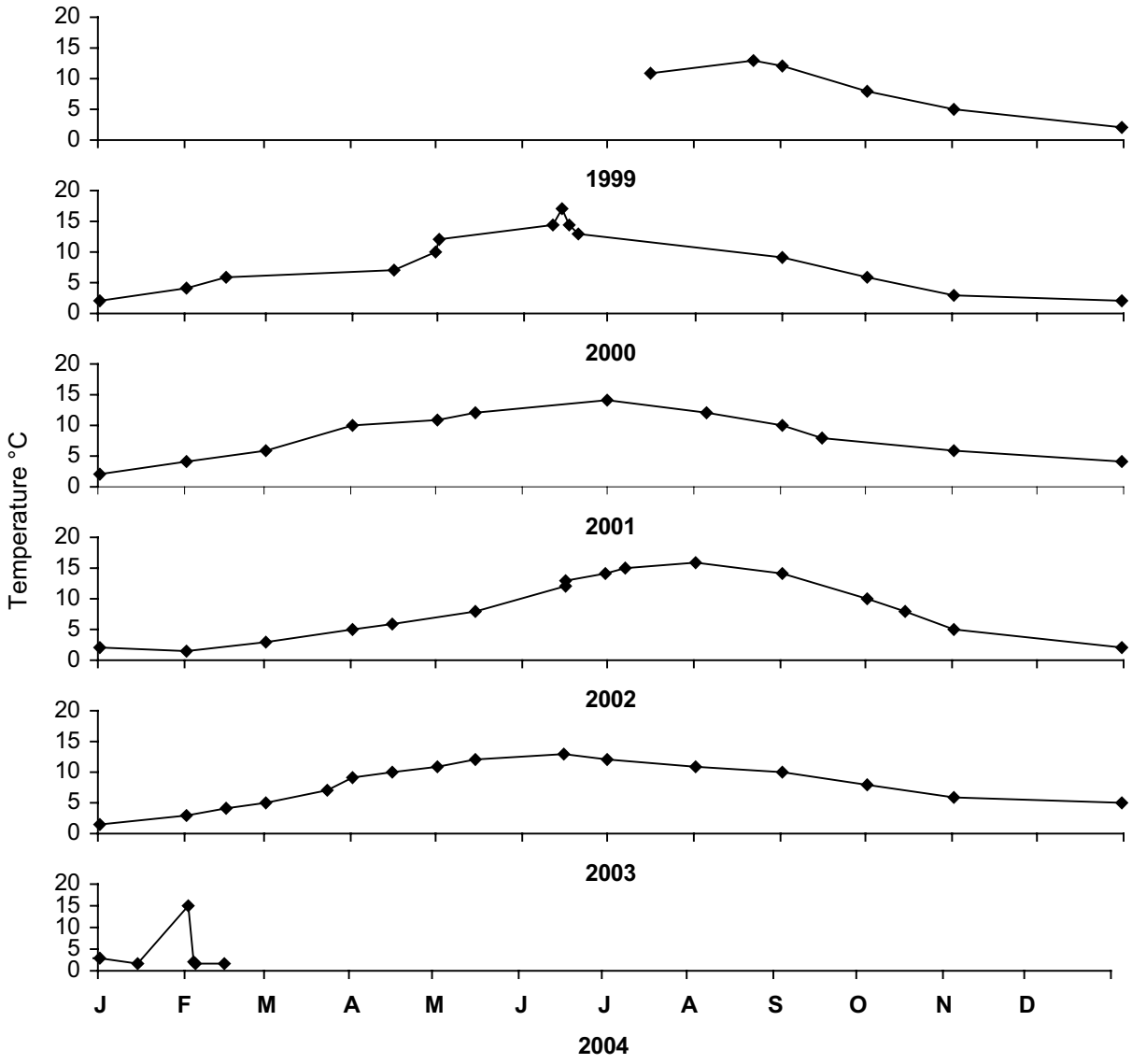


Figure 1. Simulated laboratory incubation temperature of San Miguel River for years 1999–2004. First egg masses entered Living Stream® on 16 July 1999. Maximum and minimum temperatures were 17 and 1.5°C. Temporary coolant malfunction occurred during the week of 01 February 2004 when temperature reached 15°C and was slowly cooled down to 1.5°C.

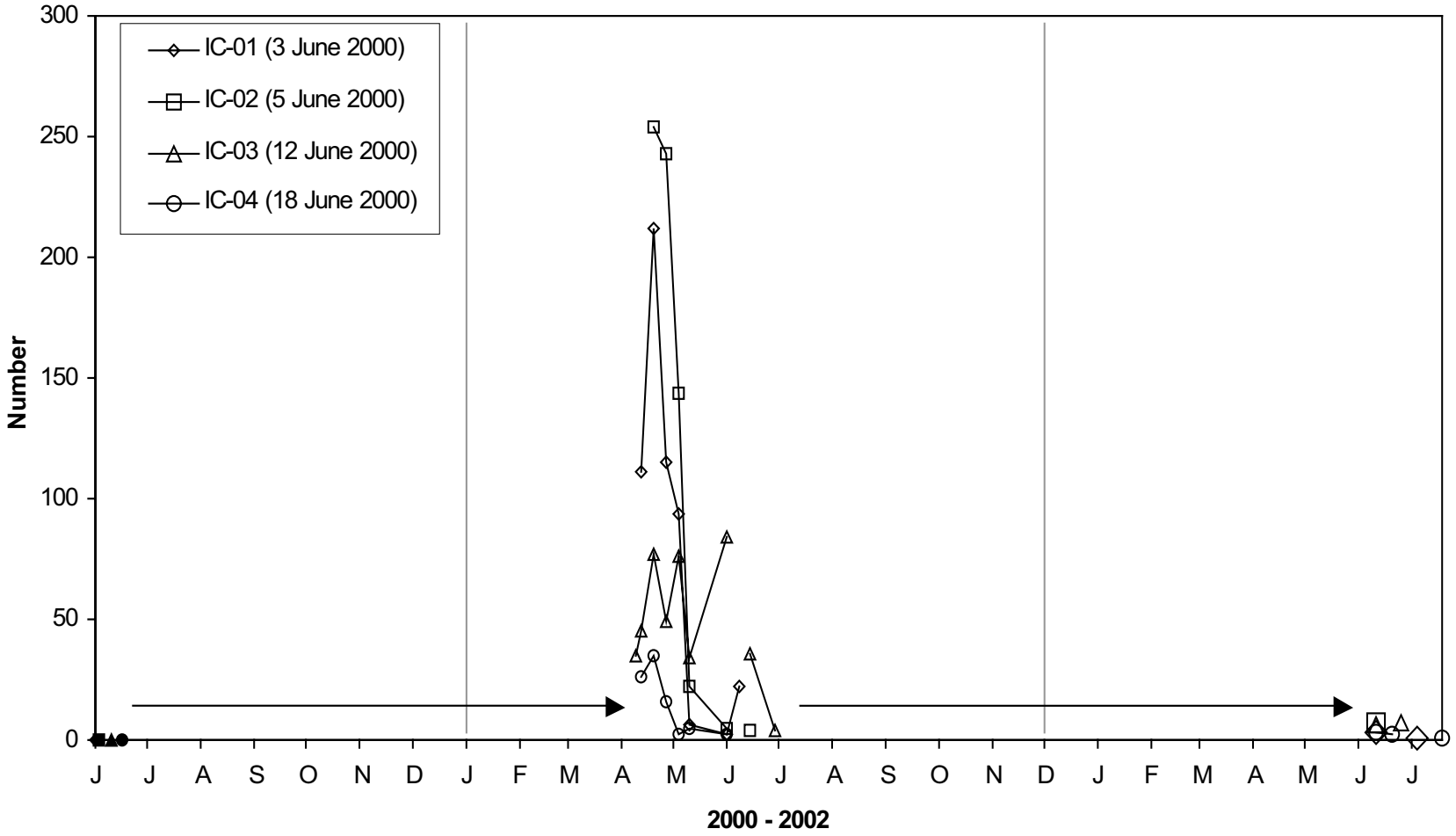


Figure 2. Hatching of four *Isogenoides colubrinus* egg masses from 4 females collected from Yampa River, CO. Egg mass totals before hatching were IC-01 (N=801), IC-02 (N=906), IC-03 (N=572), and IC-04 (N=251). Egg mass depositions indicated by filled symbols (2000), diapause indicated by horizontal arrows.

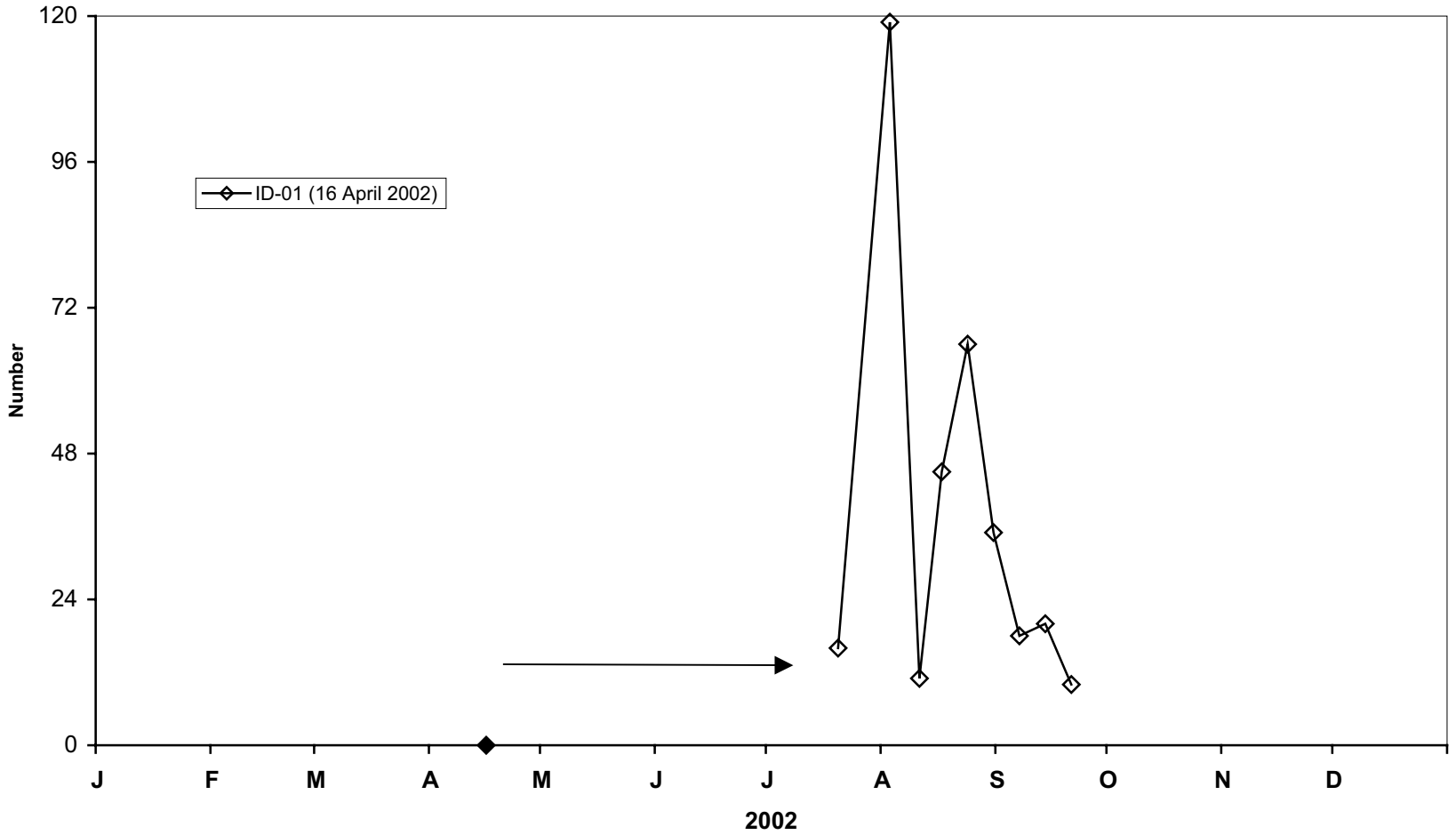


Figure 3. Hatching for one *Isogenoides doratus* egg mass from female collected at Rock River, IA. Egg mass total before hatching was ID-01 (N=996). Egg mass deposition (16 April 2002) indicated by filled symbol, diapause indicated by horizontal arrows.

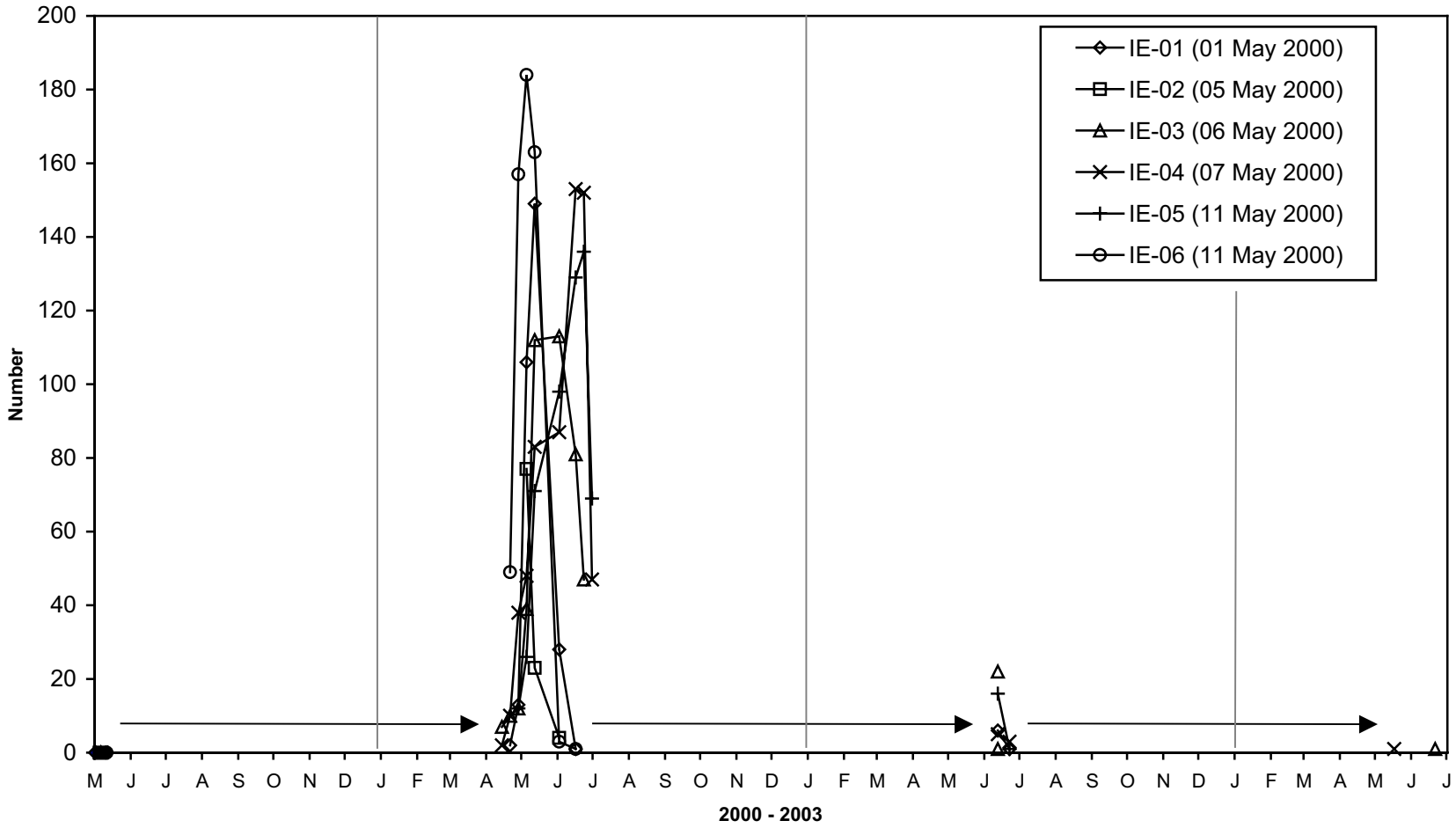


Figure 4. Hatching for six *Isogenoides elongatus* egg masses from 6 females collected from Colorado River, CO. Egg mass total before hatching were IE-01 (N=531), IE-02 (N=436), IE-03 (N=859), IE-04 (N=967), IE-05 (N=848), and IE-06 (N=608). Egg mass depositions indicated by filled symbols (2000), diapause indicated by horizontal arrows.

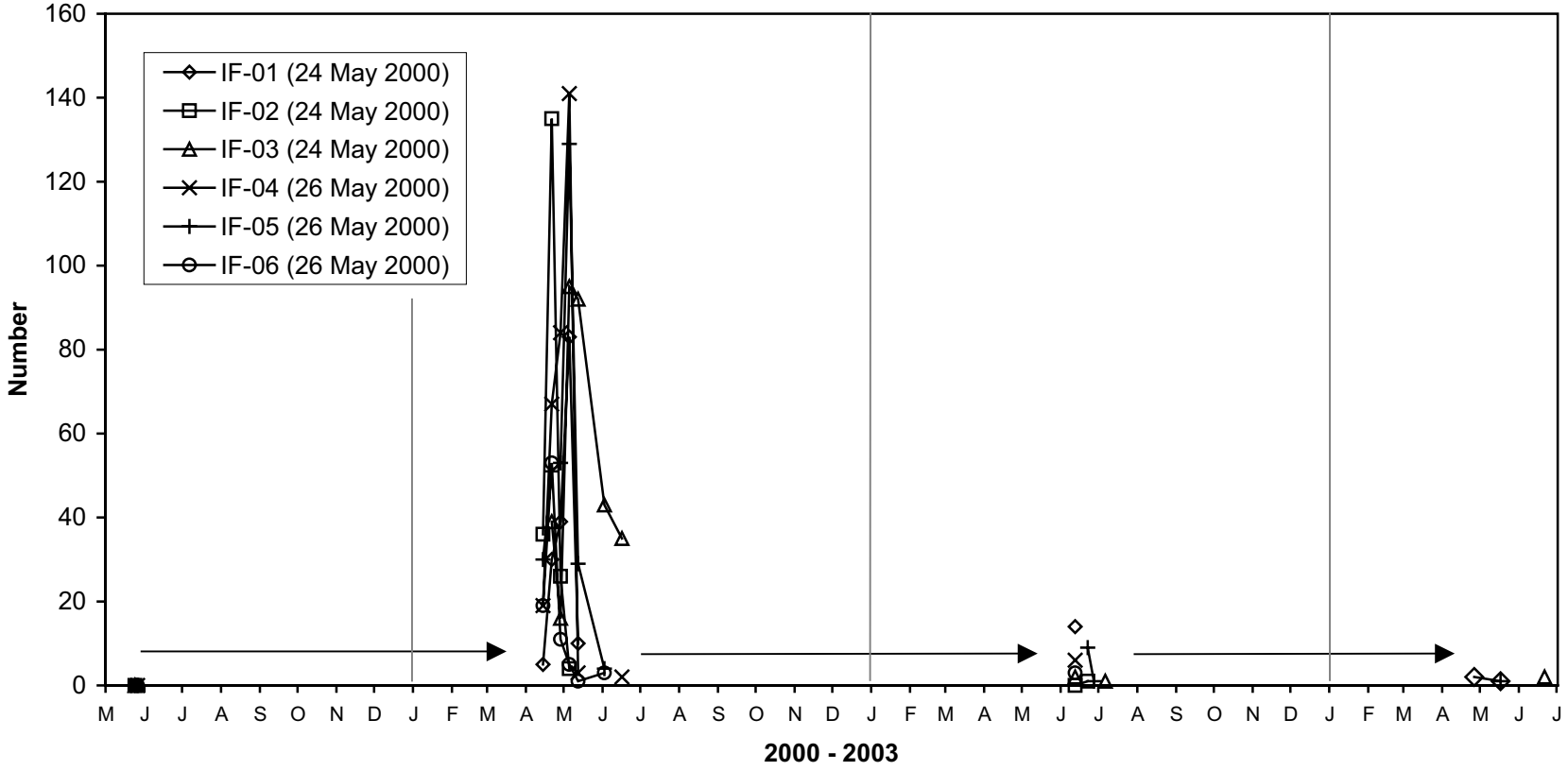


Figure 5. Hatching for six *Isogenoides frontalis* egg masses from 3 females collected at Rocky Run Cr. and 3 females collected from Fish Cr. WI. Egg mass totals before hatching were IF-01 (N=532), IF-02 (N=614), IF-03 (N=395), IF-04 (N=364), IF-05 (N=383), and IF-06 (N=200). Egg mass depositions indicated by filled symbols (2000), diapause indicated by horizontal arrows.

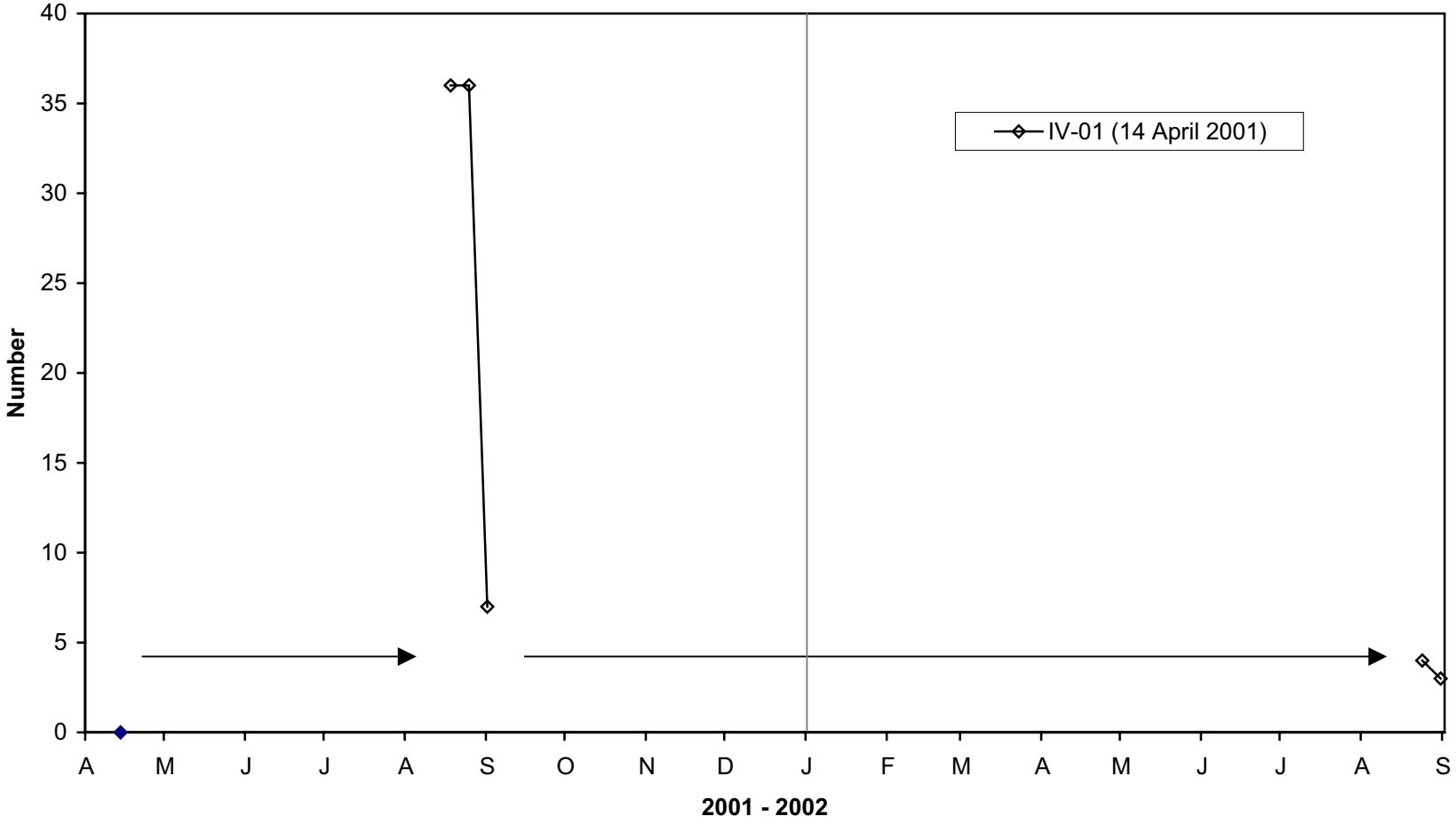


Figure 6. Hatching for one *Isogenoides varians* egg mass from 1 female collected at Big Otter River, VA. Egg mass total before hatching was IV-01 (N=94). Egg mass deposition (14 April 2001) indicated by filled symbol, diapause indicted by horizontal arrows.

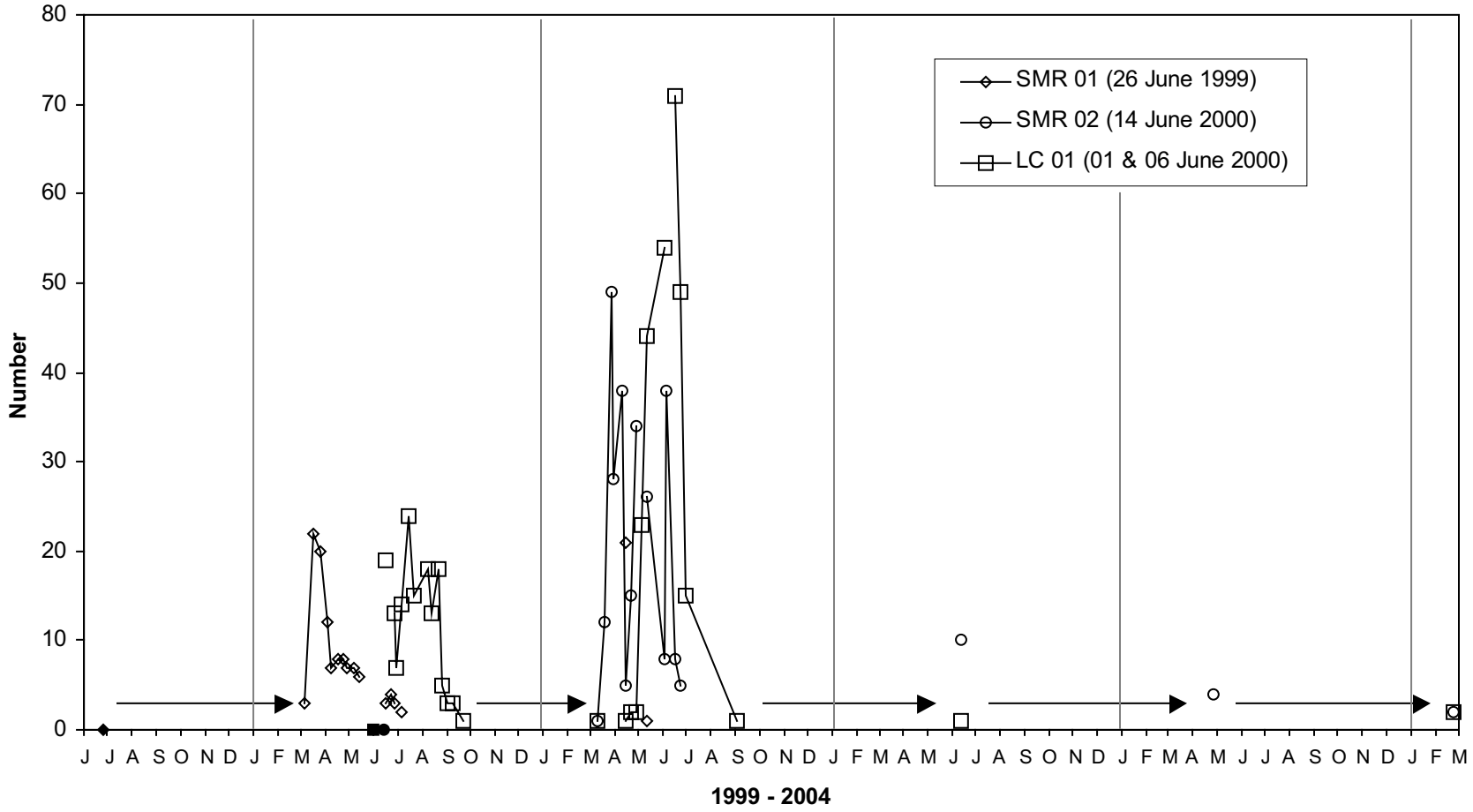


Figure 7. Egg hatching for two *Isogenoides zionensis* egg masses from 2 females collected from San Miguel River (SMR), CO, and two egg masses from 1 female collected at Leopard Creek (LC), CO. Egg mass totals before hatching were SMR 99-01 (N=368), SMR 00-04 (N=733), and LC 00-04 (N=1092). Egg depositions indicated by filled symbols (1999-2000), diapause indicated by horizontal arrows.

CHAPTER 5

LIFE HISTORY OF THE STONEFLY *Isogenoides zionensis* (PLECOPTERA: PERLODIDAE) FROM THE SAN MIGUEL RIVER, COLORADO

Introduction

The Perlodidae is a large and important family of stoneflies in North American stream ecosystems. It contains 30 genera and 122 species in the two subfamilies Isoperlinae and Perlodinae, and is unique taxonomically, from the perspective that half of its genera are monospecific. In terms of species numbers, the Isoperlinae genus *Isoperla* has experienced the greatest radiation, with well more than 60 species (Stark 2001b, S.W. Szczytko, personal communication), and *Isogenoides* is the largest Perlodinae genus with eight currently recognized species (Chapter 2). Except for *Isoperla*, adults are largely nocturnal, cryptic during the day, and generally little is known of their behavior and longevity other than anecdotal observations of times and places of discovery by collectors.

Of the 61 Perlodinae species, detailed studies of life histories have been reported for only six (10%): *Diploperla robusta* Stark and Gaufin (McCaskill and Prins 1968), *Hydroperla crosbyi* (Needham and Claassen) (Oberndorfer and Stewart 1977), *Kogotus modestus* (Banks) (Stewart and Sandberg 2003), *Malirekus hastatus* (Banks) (Huryn and Wallace 1987), *Megarcys signata* (Hagen) (Taylor et al. 1999), and *Skwala americana* (Klapálek) (Short and Ward 1980, Hassage and Stewart 1990, DeWalt and Stewart 1995). Life histories of the remaining 90% of species for this subfamily are unknown or the knowledge limited to adult presence reports or notes on certain aspects

of their biology such as food habits or nymphal growth; the life histories of representatives of 10 genera are totally unknown (Stewart and Stark 2002).

Isogenoides is widely distributed, with the five eastern species (Chapter 4) from Atlantic Canada and Minnesota south to Mississippi and South Carolina, and the three western species throughout the western cordillera and Pacific Northwest from Alaska to Saskatchewan and northern California southward to New Mexico. Populations of *I. frontalis* (Newman) from the east and *I. colubrinus* (Hagen) from the west form a transcontinental distribution across Canada. The species are usually found in small mountain rivers and their tributaries, having good water quality, but populations of some western species are able to inhabit large silty rivers with unstable substrates. In western streams they can be the lone large perlodid, or often they coexist with *Diura knowltoni* (Frison) or *Skwala americana* (Klapálek). Relatively little is known about *Isogenoides* life histories and ecology, with only one published study of nymphal growth for the eastern *I. olivaceus* (Haro et al. 1994), an unpublished thesis on life history of a Utah population of *I. zionensis* (Shakarjian 1997), and a partial life history of *I. zionensis* reported from the Rio Conejos of Colorado by DeWalt and Stewart (1995).

Isogenoides zionensis is a widely distributed western species, with only two known collection localities as far north as British Columbia and the Northwest Territories. The remainder of its usual distribution is southwestern in the “four-corner” states of Arizona, Colorado, New Mexico and Utah. Stark et al. (1986) reported Alaska as part of the distribution, but no known museum, personal holding, or other published records can be located to support this. Large populations of *I. zionensis* have been found in the following locations in Colorado: Blue River-Summit County, Rio Conejos-

Conejos County, and the San Miguel River-San Miguel County. A fourth location investigated during this study, the Uncompahgre River, Montrose County, supports a smaller population of *Isogenoides*, but until males are reared the species identity remains tentative. Shakarjian (1997) determined that *I. zionensis* had a univoltine life cycle and that egg development was direct for a Virgin River, Utah population. DeWalt and Stewart (1995) reported a 9–10 month egg diapause and a semivoltine life cycle for a Rio Conejos population. The purpose of this study was to complete an ecological investigation of *I. zionensis* from a known large population in the San Miguel River, to provide more information about its egg diapause, nymphal growth, emergence, adult riparian resting habitat, egg mass details, and oviposition. Eggs collected during this 1999-2000 study were incubated over an extended four years and adults reared from nymphs were utilized in drumming experiments. Results of those experimental protocols are reported separately in Chapter 4.

Study Stream

This study was conducted on the middle reach of the San Miguel River, at and below the Placerville bridge on Hwy 145, San Miguel County, Colorado. The San Miguel River is approximately 129 km long and originates from high elevation streams on Wasatch Mountain and Telluride Peak in the Uncompahgre National Forest and the alpine basins, Ophir and Trout lakes. It flows northwest through Montrose County, merging with the Dolores River, 11.3 km west of the historic mining town, Uravan. San Miguel River study sites were located at the Placerville bridge (2,286 m elevation) and approximately 100 m downstream, the San Miguel River Camp Site, and at the confluence with Specie Creek at M44 Rd. intersection on Hwy 145, ca. 9.7 km west of

Placerville (Fig. 1). The substrate consists mostly of cobble and gravel riffles with larger rock-rubble to boulder substrates intermixed. The riparian forest is dominated by Cottonwood (*Populus* sp.), Willow (*Salix* sp.) and Alder (*Alnus* sp.), with scattered Gambel Oak (*Quercus gambelli*), Utah Juniper (*Sabina utahensis*), Engelman Spruce (*Picea engelmanii*) and Oregon Grape / Grape Holly (*Mahoula fremontii*).

Materials and Methods

Physical Conditions

Stream and ambient temperatures were recorded each sampling date using a mercury thermometer. A Ryan® temperature monitor Model RL100™ (Ryan® Instruments, Redmond, WA, http://www.ryaninst.com/) was attached with stainless steel cable to tree roots on the South bank of the San Miguel River below the Placerville bridge. The RL-100™ was programmed to take five measurements daily and was placed into the river on July 15, 1999 and removed nearly one year later on July 9th, 2000. Stream flow data for the Placerville USGS station: 09172500 were downloaded from the following web location: [http://water.usgs.gov/pubs/wdr/wdr-CO-03-1/vol2/html/09172500.2003.sw.html].

Adult Emergence

Emergence period and frequency were determined from last instar exuviae collected from Placerville bridge abutments (Fig. 1). A single sample of residual exuviae, representing an estimate of the entire 1998 adult population was collected on 11 June 1999, 10 days before the 1999 emergence began. Fresh exuviae collections were then conducted from daily to three-day intervals, beginning June 20th and ending

July 9th when no more exuviae were found. This yielded a precise time-line of emergence for 1999. At the same times, a count of male and female adults was conducted to estimate adult presence. A third, single sample of residual exuviae representing an estimate of the 2000 adult population, was collected on July 8th, 2000, after no emergence activity and no more nymphs could be detected. This final sample is smaller than previous years because of decreased flow that year, and the majority of exuviae were located on the now-exposed and dry cobble-rock-rubble river substrate. On July 1st and 2nd, 1999, nymphal emergence and adult resting habitat were documented at the Specie Creek study area (Fig. 1) using a video camera. A sex specific line chart was constructed for both exuviae and adults, collected and observed from Placerville bridge abutments.

Oviposition, Fecundity, Longevity and Egg Incubation

Mature *I. zionensis* nymphs from San Miguel River and adjacent tributary Leopard Creek (Fig. 1) were field-reared in two 54-quart coolers partially submerged and anchored by placing rocks inside and around them in Quartz Creek, Pitkin, Colorado. Inside coolers were sheets of foam with circular holes that held foam cups partially filled with gravel substrate. Cups were covered with labeled plastic lids and examined daily for adults. Virgin adults were transferred individually to dry cups containing pieces of slightly wetted paper towel for determination of longevity and obtaining eggs for incubation experiments, and for an associated study of drumming behavior (See Chapter 3, 4).

Mating was observed but not videotaped. After the mated females produced their first egg mass, it and males were removed. Egg masses were either preserved in

75% ethanol (EtOH) or contained inside small glass vials with 100 μm mesh plastic bolting cloth held over openings with modified lids for incubation (Fig. 2). Two egg masses deposited in June by reared and mated *I. zionensis* females from the San Miguel River were incubated in 1999 and 2000 through 2004. The first year's results are reported here. Egg incubation vials were initially placed into the field-rearing chambers and kept in Quartz Creek, Colorado, where temperature was recorded daily. At the end of the 1999 field season, the eggs, that were thought to be diapausing, were transported to the University of North Texas and placed into a Living Stream® controlled environment (Frigid Units Inc.®, Toledo, OH, http://www.frigidunits.com/). During the 1999 study year, Living Stream® temperature was adjusted to near San Miguel River field conditions estimated from periodic measurements at the study site. Beginning in late July 2000, Living Stream® temperature was adjusted weekly to average temperatures recorded the previous year by a Ryan® temperature monitor Model RL-100™ (Ryan Instruments, Redmond, WA, http://www.ryaninst.com/). Monthly light/dark cycles for the Living Stream® were obtained from the Internet at [http://www.sunrisesunset.com/]. First instar nymphs obtained from hatching experiments above, were preserved in 75% EtOH for later description.

Fecundity was estimated from number of egg batches deposited and number of eggs per batch. No attempt was made to enumerate the remaining eggs inside the ovarioles. Mated females were held as described above, but placed inside an empty cooler near Quartz Creek until all egg batches were collected and females expired.

Nymphal Growth

Seasonal growth was determined from qualitative nymph samples taken from June 1999 through July 2000. Sample collection ranged from monthly during warm months to tri-monthly during winter, and total monthly numbers collected ranged 8–228. Samples were collected by kicking mineral and organic substrates upstream from a coarse (800 x 900 μm) mesh, triangular dip net. Early instars were collected on May 29, 2000, using a modified two-stage kick net with coarse first stage (800 x 900 μm) and variable (200 x 200, 140 x 200, and 60 x 60 μm), fine mesh second stage. A terminal and removable plankton bucket (63 μm mesh) was attached to the second stage to facilitate sample removal. The two-stage net was anchored in shallow, slow current with steel rods and upstream substrates were agitated and removed with a sharpshooter spade to a depth of approximately 30 cm. Preserved samples taken back to the laboratory were floated in strong saltwater solution to separate organic from mineral debris and the organic debris was completely examined for early instars at high power (50x) under a dissecting microscope.

Interocular distance (IOD, the minimum distance between the eyes) of nymphs was measured with a calibrated ocular micrometer fitted to the stereo-dissection microscope. Gender of middle to late instar nymphs was determined by the presence of a gap in the posterior setal margin of the eighth sternum of females (Stewart and Stark 2002). A sex specific line chart was constructed by placing male and female nymphs into 0.02 mm size classes and graphing the mean IOD and standard deviation for each month. Additional first instar laboratory hatching data from extended incubation

experiments were added to provide greater detail in deciphering growth classification (See Chapter 4).

Results and Discussion

Stream discharge and temperature were variable, depending on depth of snow pack and spring weather. In the study-years 1999 and 2000, peak levels occurred in late-May to early-June, and temperature ranged from -2°C in late January 2000 to 21°C in mid-July, 1999 (Fig. 3).

Other stoneflies collected within the study area included *Alloperla pilosa* Needham & Claassen, *Amphinemura banksi* Baumann & Gaufin, *Claassenia sabulosa* (Banks), *Cultus aestivalis* (Needham & Claassen), *Diura knowltoni* (Frison), *Hesperoperla pacifica* (Banks), *Isoperla fulva* Claassen, *Isoperla quinquepunctata* (Banks), *Malenka coloradensis* (Banks), *Paraleuctra vershina* Gaufin & Ricker, *Paraperla frontalis* (Banks), *Perlomyia utahensis* Needham & Claassen, *Pteronarcella badia* (Hagen), *Skwala americana* (Klapálek), *Suwallia pallidula* (Banks), *Sweltsa coloradensis* (Banks), *Triznaka pintada* (Ricker) and *Triznaka signata* (Banks).

Other dominant insect genera, tribes and families associated with *I. zionensis* in the San Miguel River included: EPHEMEROPTERA: *Acentrella* sp., *Baetis* sp., *Cinygmula* sp., *Drunella doddsi* (Needham), *Drunella grandis* (Eaton), *Epeorus* sp., *Rithrogena* sp.; COLEOPTERA: *Brychius* sp., *Narpus concolor* (LeConte), *Helichus striatus* LeConte, *Optioservus castanipennis* (Fall), Coleoptera: Tribe Hydroporini, *Zaitzevia parvula* Horn; TRICHOPTERA: *Apatania* sp., *Arctopsyche grandis* (Banks), *Brachycentrus occidentalis* Banks, *Glossosoma* sp., *Lepidostoma* sp., *Rhyacophila* sp.;

DIPTERA: *Antocha* sp., *Atherix pachypus* Bigot, Chironomidae, *Dicranota* sp., Dolichopodidae, *Hexatoma* sp., *Simulium* sp., and *Agathon* sp..

Adults.— The *I. zionensis* emergence was well synchronized, occurring over a 20 day period, from late June to early July, 1999 (Fig. 4). The vertical bridge abutments near Placerville were primary transformation sites for the river population during spring flows, and the periodic field exuviae collections gave a precise time-line for emergence of the local population. Exuviae were first observed and collected on June 20, 1999 when river temperature was 12°C at noon and 15°C at 16:00 (Fig. 4). The actual sex ratio (male:female) for 1999 adults was 1.85:1 (N=1331). Total exuviae sex ratios, collected on 11 June, 1999, for the estimated 1998 adults was 1.21:1 (N=736), and July, 8, 1999 collection for the estimated year-2000 adults 0.71:1 (N=246). Emergence in 1999 was not protrandrous with both sexes of adults and exuviae simultaneously observed at the beginning. Maximum numbers of exuviae were observed four days apart, with males first on June 27, followed by females on July 1, 1999. The peak numbers of female exuviae and adult presence coincide with oviposition flights observed two and four days later. Adult presence was estimated using counts of live adults found on the Placerville bridge abutments at the same time that exuviae counts were made (Fig. 4).

The San Miguel River *I. zionensis* population began their 1999 emergence 12 days earlier than a Rio Conejos population in Colorado (DeWalt and Stewart 1995). San Miguel River emergence and adult presence ranged June 20–July 9, 1999. Rio Conejos presence ranged June 8–June 28 (1988–1989), emergence was not protrandrous, and sex ratio was heavily skewed towards males.

Emergence was largely over and nymphs gone on July 15th, 1999, when average daily temperature reached 21°C. On July 1, 1999, nymphs began to exit the river at the Specie Creek study area at 21:30, one-half hour after a large, hovering, cloud-like hydropsychid hatch had occurred. The transformation process for one female lasted 21 minutes; after final exit from the exuvium she rested approximately 40 minutes with wings hanging downwards, while her body hardened. Nymphs continued to leave the river until approximately 00:30. DeWalt and Stewart (1995) observed a similar time for transformation from 20:30 to about 22:00. Teneral adults were bright yellow with smoky-gray wings held perpendicularly erect over the body still wrinkled and wet. The majority of observed teneral adults carried minute, orange mites (Hydrachnida) around the wing bases. Most adults, after hardening, moved over rocks and boulders to reach woody vegetation where they crawled upwards.

On July 2nd, 1999, from 09:00 to 12:00 a search of streamside vegetation consisting mostly of young willows and alder was conducted to find the resting habitats of adults that emerged the previous evening. At the emergence site, near the mouth of Specie Creek, many fresh exuviae were still attached to rocks, boulders and only a few young saplings, and a beating sheet was used in an attempt to collect adults from the nearby streamside vegetation. Since none were found, adult searching was moved inland, away from the river. From 12:00 until 14:00, when ambient temperature climbed from 24–29°C, numerous adult males and females were observed from 10–50 m inland, at heights of 1–2 m, under loose bark of mostly alder and cottonwood trees. DeWalt and Stewart (1995) observed emergence occurring < 1 m from the ground and found adults in willows either at the bases in the morning or near the tops as the sun rose.

Sexes are therefore probably aggregated as “bushtoppers” (Stewart 1994) and males find females through duetting with vibrational communication on woody substrates (Stewart 2001).

Oviposition was observed and videotaped near the Placerville bridge on July 3rd, 1999, from 11:30 to 14:00. Forty-three ascending and descending, “undulating”, flights were observed either originating from the riparian forest vegetation to the water or returning from the water back to the forest. Ambient temperature increased from 25°C at 09:00 to 31°C at 12:15, river temperature held constant at 11°C, and the sky was variable throughout the day, from slightly cloudy to clear and sunny. The tallest trees observed in return flights were engelman spruce, estimated to be between 23–30 m in height. Descending *I. zionensis* females were observed landing on the river surface and were quickly swept from view. I have interpreted this behavior to indicate that females release eggs on water contact although the flights were of such height, quickness and over the river that females could not be caught before and after touching the water to verify this. DeWalt and Stewart (1995) did observe females fluttering on the surface of the Rio Conejos, Colorado, to release their black egg masses. In interesting contrast during the same San Miguel River observation period, female *Pteronarcella badia* were observed releasing and dropping egg masses from about 2 m above the river.

Females emerge with eggs nearly mature. Nine females ranging in age from several hours to six days were successfully mated with males held in foam cups. These experimental females produced up to three egg masses with total eggs per female (fecundity) ranging from 549–1093 (Table 1). Their first and second masses had

average number of eggs of 499.2 ± 176.1 and 175.5 ± 78.9 respectively. These first masses took several hours to nine days to be extruded from the genital opening located at the rear of the 8th sternum. Three females, whose ages ranged from several hours to 6 days at the time of mating, produced a third egg mass that had a lower average count of 50.0 ± 22.9 eggs and took an average of 7.7 ± 3.2 days to be produced after mating (Table 1).

These egg mass results compare favorably in number of egg masses produced per female with those reported by DeWalt and Stewart (1995), but averaged fewer per 1st, 2nd, and 3rd mass. Several natural variables such as degree day accumulation and nymphal diet may help to explain the 27–85% difference in fecundity between the San Miguel River and the Rio Conejos (DeWalt and Stewart 1995), Colorado populations.

Longevity was observed for 26 males and 22 females experimentally obtained from Quartz Creek field-rearing chambers. Adults emerged from June 21, to June 26, 1999 and 26 males lived an average 6.8 ± 2.8 days (range 1–12), and 22 females averaged 8.1 ± 3.0 days (range 2–13).

Egg Development. — The 1999 incubated eggs underwent at least an 8-month diapause (Fig. 5), and protonymphs began eyespot development shortly before hatching (Fig. 6). As these eggs hatched in the year 2000, average interocular distance decreased slightly from March ($\bar{x}$=0.26 ± 0.04 mm, N=35) to June ($\bar{x}$=0.22 ± 0.18 mm, N=10). These eggs continued hatching in April-May, 2001 (N=22), after a second, approximately 22-month diapause.

Nymphs.— First instars (Fig. 7) were unpigmented, had nine antennal and three cercal segments, and overall mean interocular distance was 0.22 ± 0.2 mm (N=114).

Early instar nymphs (N=109) first appeared in the river May 29, 2000 (Fig. 5) when average stream temperature was 8.5°C, and incubation experiments indicated that these were from the previous year eggs. Nymphal growth rates were exponential when transposing the June, 2000 field-collected and March–July, 2000 laboratory-hatched, early instars onto the 1999 growth curves (Fig. 5). Nymphs were approximately half grown by October to December, and greatest growth occurred from June to December and decreased from March to June (Fig. 5). Fastest growth occurred initially as temperature began to decrease from 13°C in July, to 0.5°C in December 1999. Slowed growth occurred during the coldest months (December–March) then decreased until emergence.

Nymphs reached maximum size on March 12, 2000 when temperature was 3°C. As temperature increased to only 8°C on June 24, growth declined until emergence in late June. The decline in growth was possibly due to small sample size, or that the larger, more developed nymphs moved to different microhabitats and escaped sampling or had already emerged. Several larger, more developed nymphs (interocular distance > than 2.6 mm ♂, and 3.2 mm ♀) were collected during this period of declining growth and adults had begun to emerge. A large size range throughout the seasonal growth period was observed as previously reported in other studies (Hynes 1970, Oberndorfer and Stewart 1977). Differential growth rates, extended egg hatching or recruitment periods, and sexual dimorphism among individuals probably contributed to the observed range in size of nymphs.

Nymphs were primarily collected from under cobble-rock-rubble substrates and, from gravel to cobble-sized substrates from under-cut banks. *Isogenoides zionensis* early instars were collected from shallow hyporheic gravel habitats.

From the Shakarjian (1997) study and my observations of direct hatching in a nearby Leopard Creek population (Fig. 1) to extended diapause in San Miguel River population and Rio Conejos population (DeWalt and Stewart 1995), it appears that *I. zionensis* has a great capacity for egg development ranging from direct hatching to diapause over several years (Chapter 4) resulting in either univoltine or variable-length semivoltine life cycles. The currently available data from these studies suggest this range may be genetically determined and expressed in a single egg mass from a female, or that given populations may, due to temperature regimes, or other factors, have adopted a homodynamic, heterodynamic, or combination egg development strategy. The lack of direct hatch of year 1999 and 2000 eggs in this San Miguel River population suggests that it has adopted a semivoltine strategy.

Table 1. *Isogenoides zionensis* experimental egg mass collection for nine captive-bred females reared at Quartz Creek, Gunnison County, CO, June-July, 1999. Number of eggs / mass and number of days after copulation for each mass deposition.

	Number of Eggs / Mass for up to Three Masses and (Number of Days after Copulation) For Nine Gravid Females									
♀ (age at mating in days)	**1**(6)	**2**(2)	**3**(0)	**4**(6)	**5**(4)	**6**(3)	**7**(2)	**8**(0)	**9**(0)	**($\bar{x}$ ± SD) numbers and days**
1st Egg Mass	442	670	372	391	500	400	401	416	901	499.2 ± 176.1
	(7)	(0)	(1)	(1)	(2)	(1)	(0)	(1)	(1)	(1.6 ± 2.1)
2nd Egg Mass	67	66	153	264	307	187	171	173	192	175.6 ± 78.9
	(8)	(4)	(8)	(2)	(3)	(2)	(2)	(9)	(3)	(4.6 ± 2.9)
3rd Egg Mass	59	67	24							50.0 ± 22.9
	(9)	(4)	(10)							(7.7 ± 3.2)
Sum of Eggs / ♀	**568**	**803**	**549**	**655**	**807**	**587**	**572**	**589**	**1093**	**691.4 ± 180.1**

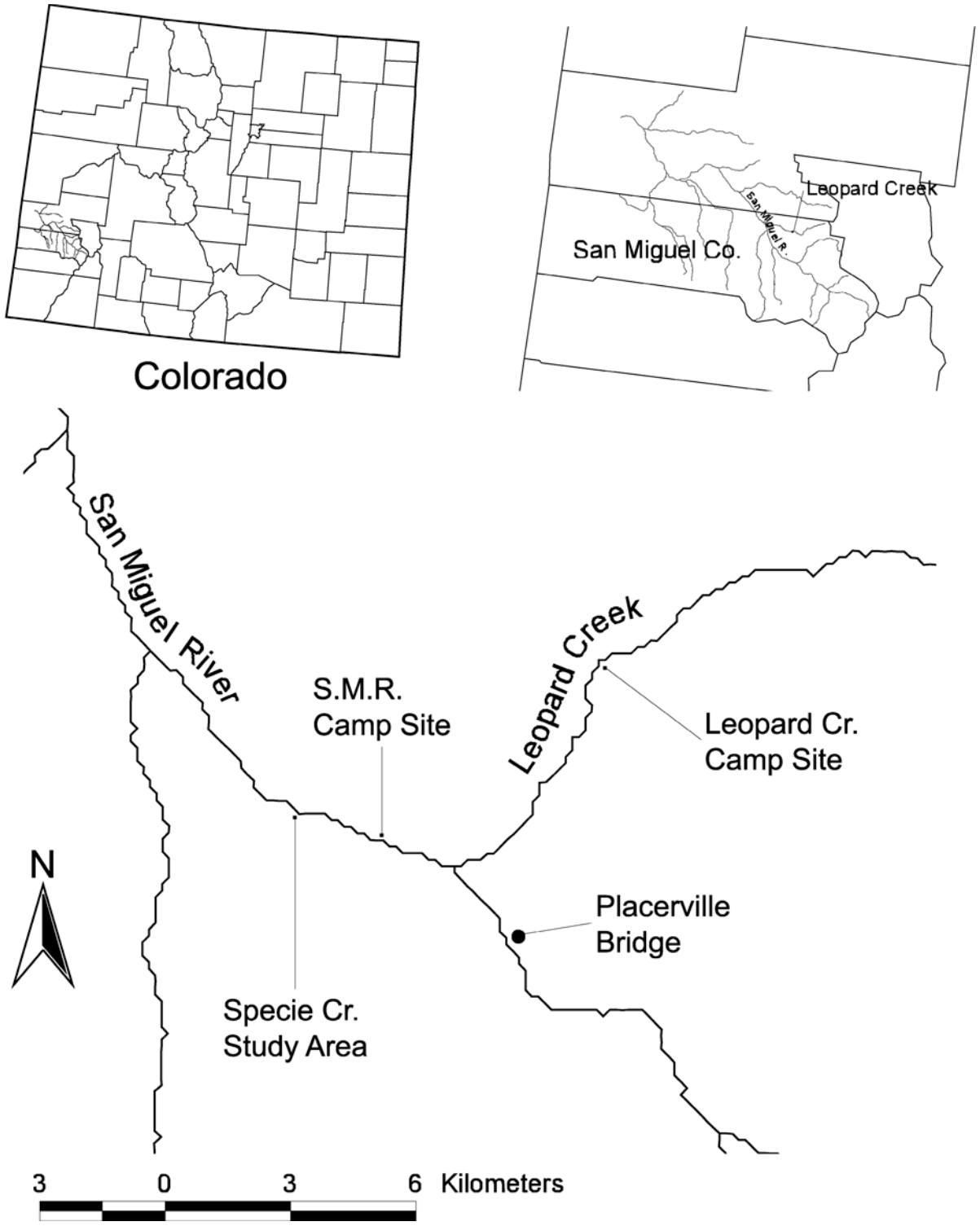


Figure 1. Maps showing the Dolores River drainage system and the San Miguel River study sites, San Miguel County, Colorado.

Figure 2. Egg incubation containers with 100µm mesh plastic bolting cloth held over openings with modified lids. Living Stream® in background.

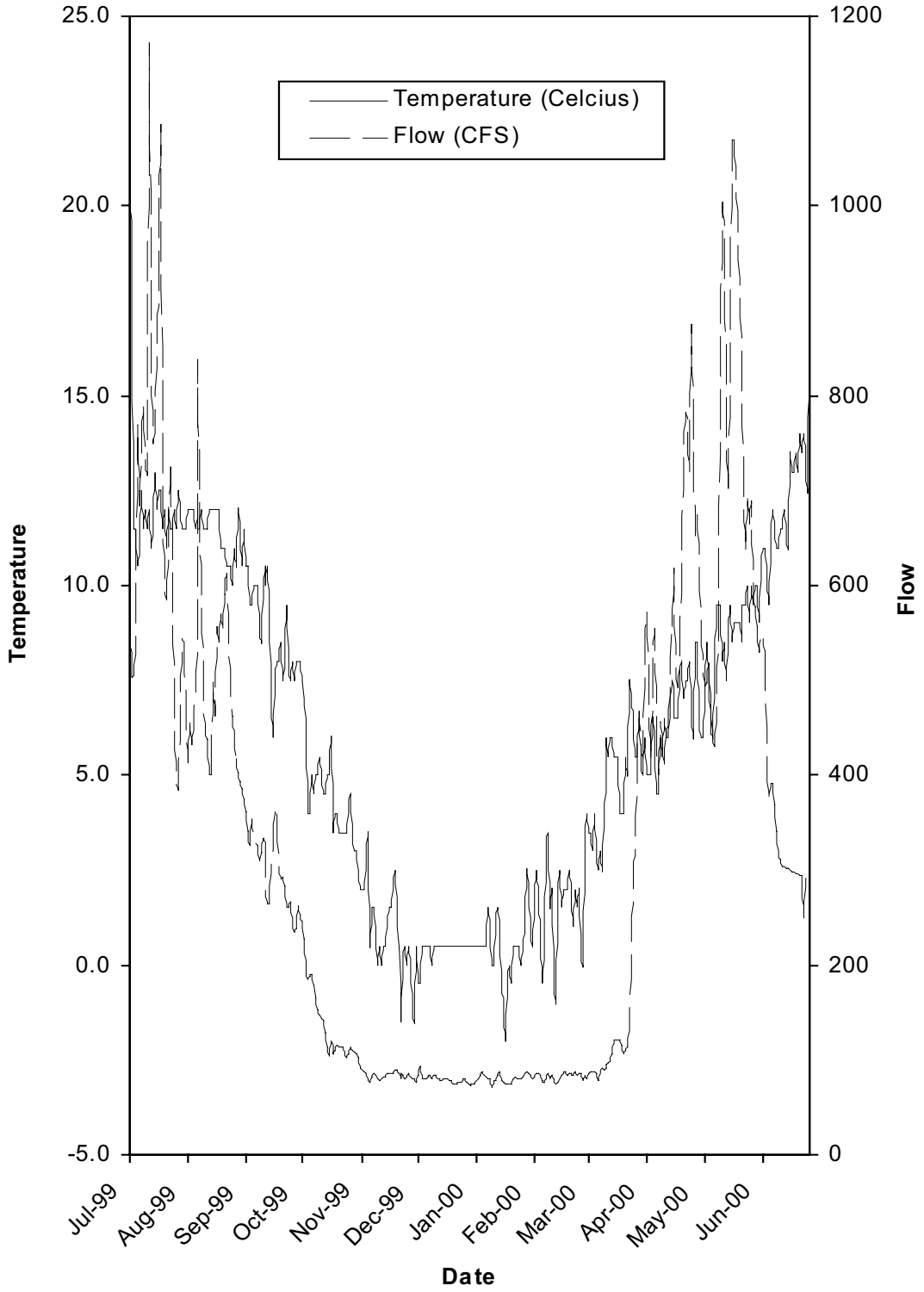


Figure 3. Average temperature (°C) and stream flow (CFS) of San Miguel River, San Miguel County, Placerville Colorado, July 15, 1999 – July 9, 2000. Stream flow data from USGS station: 09172500, near Placerville.

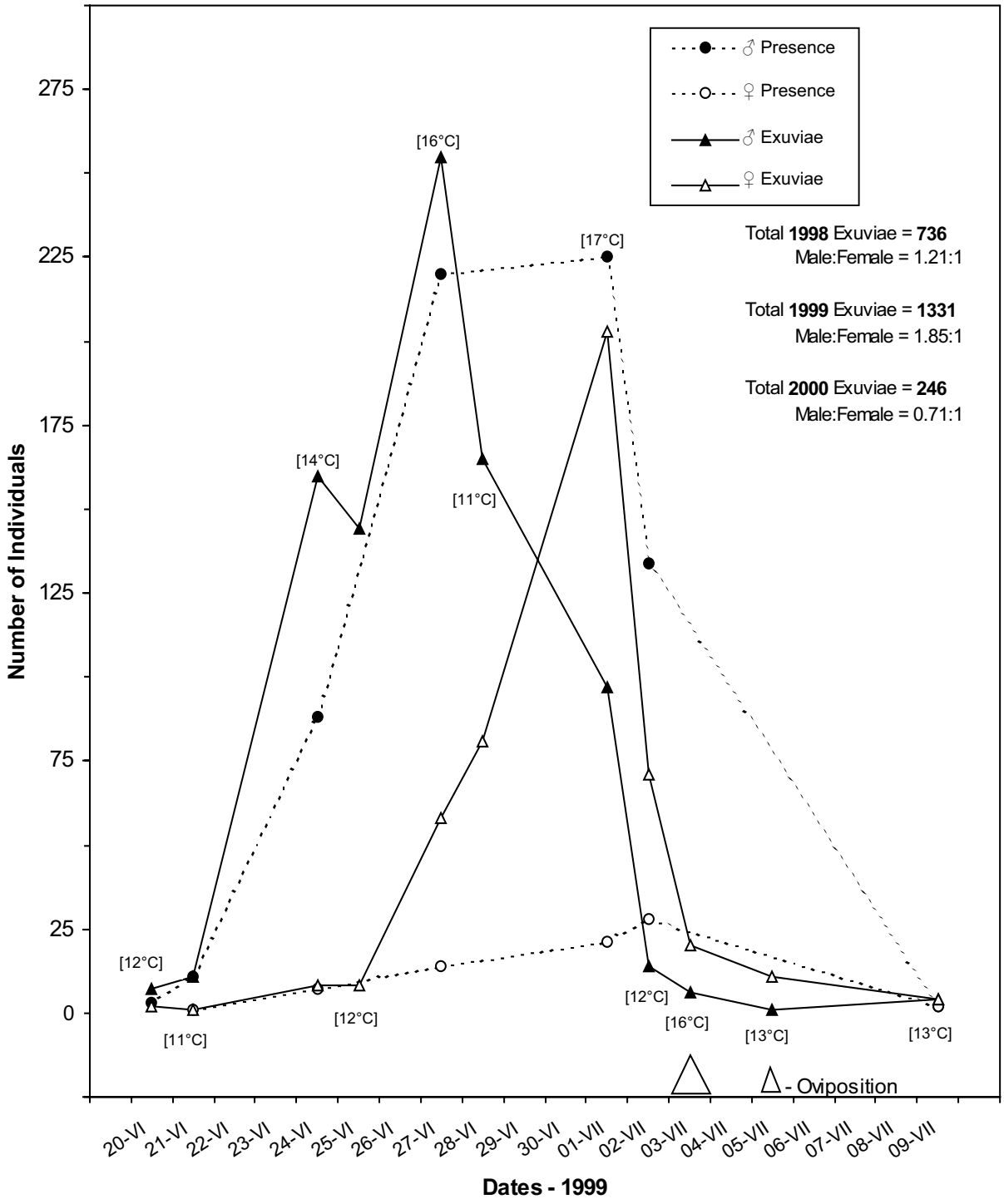


Figure 4. Male and female presence and exuviae counts from two bridge abutments on the San Miguel River, Placerville, Colorado, 1999; and total counts of residual exuviae on the bridge for years 1998 and 2000, collected on 11-VI-1999 and 08-VII-2000, respectively. 1999 oviposition observations indicated by triangles were made on 03 and 06 July, when water temperature was 12 and air temperature was 26°C.

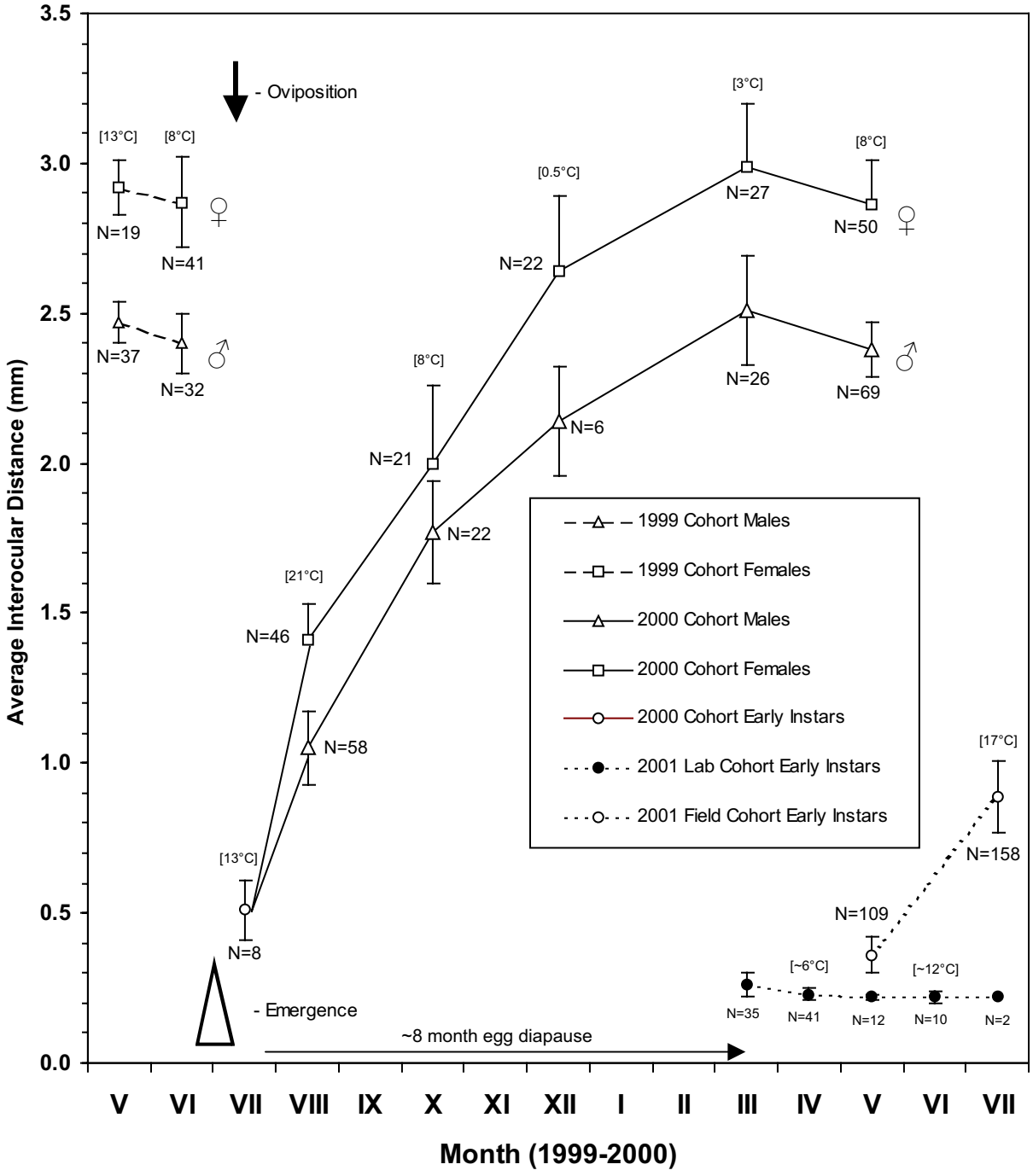


Figure 5. Average growth of 250 ♂, 226 ♀ and 375 field collected and laboratory hatched early instar *Isogenoides zionensis* nymphs from San Miguel River, Colorado, 1999-2000. Vertical bars = standard deviation, triangle = emergence (June 20th to July 9th) and vertical arrow = oviposition (3-6 July, 1999). 2001 lab cohort egg mass (N=368) underwent an approximate 8-month diapause (June 26th, 1999 to March 6th, 2000).

Figure 6. Eyespot development of *Isogenoides zionensis* protonymphs after 4-years of development.

Figure 7. *Isogenoides zionensis* first instar nymph hatching from egg showing hinged cap split from along eclosion line.

APPENDIX

Isogenoides CHARACTERS

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

Male. —
I.c. 1 Macropterous to partially brachypterous.
I.d. 1 Macropterous.
I.e. 1 Brachypterous, forewing reaching Ab_{2-3}, hindwing reaching Ab_{4-5}.
I.f. 1 Macropterous.
I.h. 1 Macropterous.
I.o. 1 Macropterous.
I.v. 1 Macropterous.
I.z. 1 Brachypterous, forewing reaching Th_3, hindwing reaching Ab_2.

2 Length of forewings 9.5–15 mm; length of body 15–20 mm.
2 Length of forewings 13–14.5 mm; length of body 13–17 mm.
2 Length of forewings 4.5–7.5 mm; length of body 16–18 mm.
2 Length of forewings 15–17 mm; length of body 17–19 mm.
2 Length of forewings 14–19 mm; length of body 14–20 mm.
2 Length of forewings 13–15 mm; length of body 15–16 mm.
2 Length of forewings 13–15 mm; length of body 15–17 mm.
2 Length of forewings 3.1–3.9 mm; length of body 16–20 mm.

3 General body color brown to dark brown.
3 General body color brown to dark brown.
3 General body color brown to dark brown.
3 General body color brown to dark brown.
3 General body color brown to dark brown and black.
3 General body color brown to dark brown and black.
3 General body color brown to dark brown and black.
3 General body color brown to dark brown.

4 Dorsum of head with thin light area along mesoanterior margin (Fig. 19);
4 Dorsum of head with rounded, light area offset from mesoanterior margin by thin brown band along anterior margin (Fig. 38);
4 Dorsum of head usually without small light area along mesoanterior margin (Fig. 58);
4 Dorsum of head with thin light area along mesoanterior margin (Fig. 77);
4 Dorsum of head with tiny, light area along mesoanterior margin (Fig. 95);
4 Dorsum of head with mesoanterior margin brown to light brown (Fig. 114);
4 Dorsum of head with variable, tiny, light area along mesoanterior margin (Fig. 133);
4 Dorsum of head variable, with or without small light area along mesoanterior margin (Fig. 152);

5 anterolateral large, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral large, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral variable, small, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral small, irregular-shaped, light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral small, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral irregular-shaped light areas variable, when present, small, between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral large, irregular-shaped light areas between anterior-most portions of M-pattern and anterolateral margins of frons;
5 anterolateral irregular-shaped light areas variable, when present, large, between anterior-most portions of M-pattern and anterolateral margins of frons;

6 large yellow, nearly triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures;
6 large yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures;
6 large yellow, narrowly rounded area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures;
6 large yellow, nearly triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

6 large yellow, broadly rounded area with base along posterior margin of head, extending mesoanteriorly past epicranial suture intersection, ending inside interocellar area;
6 large yellow area with base along posterior margin of head, extending mesoanteriorly forming slightly truncated area, a second lateral, angled area below posterior margin of eye;
6 large yellow area with base along posterior margin of head, anterolateral borders angled posteriorly, sometimes pointed, where broadly rounded mesoanterior border extends almost to epicranial suture intersection;
6 large yellow, approximately triangular area with base along posterior margin of head, extending mesoanteriorly to intersection of epicranial sutures;

7 tiny dark brown setae absent.
7 tiny dark brown setae absent.
7 tiny dark brown setae absent.
7 tiny, dark brown, erect setae sparsely scattered in basal occiput regions.
7 tiny dark brown setae absent.
7 tiny dark brown setae absent.
7 tiny dark brown, erect setae, sparsely scattered on light or yellow pigment areas.
7 tiny dark brown setae absent.

8 M-pattern raised, without setae, dark brown pigmentation beginning at anterior ocellus, fading to light brown and yellow at anterior-most portions, these blending in pigmentation with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margin of antennal bases (Fig. 19).
8 M-pattern raised, without setae, dark brown throughout most of pattern, beginning to fade to light brown and yellow just past anterior-most portions, these blending in pigmentation with light anterolateral areas of frons (Fig. 38),
distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases.
8 M-pattern raised, without setae, dark brown throughout entire pattern, not fading or blending into light anterolateral areas on frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas, blending into dark brown, almost black irregular-shaped markings along inner margins of antennal bases (Fig. 58).
8 M-pattern raised, without setae, dark brown pigmentation beginning at anterior ocellus, fading to light brown and yellow at anterior-most portions, these blending in pigmentation with light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margin of antennal bases (Fig. 77).
8 M-pattern raised, without setae, dark brown throughout most of pattern, beginning to fade to brown- light brown just past anterior-most portions, these blending in pigmentation with light anterolateral areas of frons,
distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 95).
8 M-pattern raised, without setae, dark brown throughout most of pattern, pattern not fading or blending into light brown or light anterolateral areas of frons;
distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 114).
8 M-pattern raised, without setae, dark brown throughout most of pattern, pattern not fading or blending into light anterolateral areas of frons, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas along inner margins of antennal bases (Fig. 133).
8 M-pattern variable, raised, without setae, usually medium brown throughout most of pattern, fading to light brown or yellow at anterior most portions, these blending in pigmentation with light anterolateral areas on frons, sometimes M-pattern all brown or mostly yellow extending anteriorly to labrum, distolateral-most, posteriorly directed legs intercept lateral wrinkled areas (Fig. 152).

9 Interocellar area variable, usually brown, similar to surrounding area,
sometimes darker brown pigment enters area laterally, connecting lateral ocelli to anterior ocellus,
forming two, wide, slightly angled, longitudinal bands extending anteriorly from lateral ocellus to inner, posterior margins of M-pattern (Fig. 19).
9 Interocellar area brown with dark brown pigment entering laterally,
dark brown areas connecting lateral ocelli to anterior ocellus, extending towards eyes, ending below large, lateral, medium brown rugosities;
medium brown areas above dark brown areas;
dark and medium brown areas form two, wide, slightly angled, longitudinal bands extending mesoanteriorly from lateral ocelli to inner, posterior margins of M-pattern (Fig. 38);
9 Interocellar area variable, usually brown with light brown median stripe.
sometimes slightly darker brown at least anteriorly,
usually inner-area brown pigment extends anteriorly to mesoposterior margin of M-pattern, width of medium brown area variable, reaching furthest laterally to posteriorly directed leg of M-pattern, to as close as along inner, posterior margin of M-pattern;
dark brown areas form two variable, anterolaterally directed bands extending from lateral ocelli to antennal bases (Fig. 58).
9 Interocellar area variable, usually brown with dark brown pigment entering laterally,
sometimes completely darker than background, dark brown areas when present, connect lateral ocelli to anterior ocellus, extending towards eye, ending below large, lateral, medium brown rugosities;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

dark brown areas form two, wide, laterally directed bands, extending anterolaterally from lateral ocelli, reaching at least lateral wrinkled areas (Fig. 77).
9 Interocellar area dark brown with dark brown pigment entering laterally and yellow entering mesoposteriorly,
dark brown areas connect lateral ocelli to anterior ocellus, extending towards antennae, ending before reaching large, lateral, medium brown rugosities;
dark brown areas form small X-shaped area posterior of M-pattern (Fig. 95).
9 Interocellar area brown variable, usually brown with dark brown pigment entering laterally and light brown median stripe,
dark brown irregular-shaped areas connecting lateral ocelli to anterior ocellus variable, extending directly to large, lateral, medium brown rugosities, or sometimes anteriorly to posterior margin of M-pattern;
dark brown areas usually form two short, posterolaterally directed bands, or sometimes two wide, slightly angled, longitudinal bands connecting to inner legs of M-pattern (Fig. 114).
9 Interocellar area generally medium brown with dark brown pigment entering laterally,
dark brown areas connect lateral ocelli to anterior ocellus, extending directly to large, lateral, medium brown rugosities;
dark brown areas form two short, posterolaterally directed bands (Fig. 133).
9 Interocellar area variable, generally light brown to brown with two, narrow, dark brown, transverse bands entering laterally, sometimes with narrow, light brown, median stripe,
dark brown transverse bands entering area variable in height, arise from nearly black pigment enclosing large, lateral, medium brown rugosities;
dark brown, narrow, longitudinal bands extend anteriorly to posterior margins of M-pattern;
brown, dark brown and almost black areas variable, loosely form an H-shaped dark area (Fig. 152).

10 Antennae medium to dark brown, with 50+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae.
10 Antennae dark brown, with 46+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered short, erect, golden setae.
10 Antennae medium brown, with 48+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae.
10 Antennae medium to dark brown, with 52+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae.
10 Antennae dark brown, with 45+/- segments, first two segments covered with dense, clear, clothing setae, segment two with few, short, erect, brown setae apically, remaining covered with partially erect, golden brown setae.
10 Antennae dark brown, with 46+/- segments, covered with dense, clear, partially erect, clothing setae and sparsely scattered, short, erect, golden setae.
10 Antennae dark brown to black, with 43+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden brown setae.
10 Antennae variable, dark brown to yellow, with 52+/- segments, covered with dense, clear, partially erect clothing setae and sparsely scattered, short, erect, golden setae.

11 Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown pigment;
11 Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, with almost black pigment along posterior borders;
11 Pronotum with anterior and posterior transverse furrows deep, anterior furrow filled with medium brown, almost black along its posterior margin, posterior furrow filled entirely with dark brown almost black pigment;
11 Pronotum with anterior and posterior transverse furrows deep, anterior furrow filled with slightly darker brown pigment, posterior furrow filled with dark brown with almost black, thin ridges posteriorly;
11 Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, with almost black pigment along posterior borders;
11 Pronotum with anterior and posterior transverse furrows deep, sometimes filled with slightly darker brown, almost black pigment along posterior borders;
11 Pronotum with anterior and posterior transverse furrows deep, filled with slightly darker brown, anterior furrow with short, thin almost black sutures along mesoposterior border; posterior furrow with dark brown almost black pigment along posterior border;
11 Pronotum with anterior and posterior transverse furrows deep, filled with dark brown, almost black along anterior border of anterior furrow and posterior border of posterior furrow;

12 background pigmentation light brown or brown, anterior and posterior margins dark brown;
12 background pigmentation light brown, anterior and posterior margins dark brown;
12 background pigmentation light brown, anterior and posterior margins dark brown;
12 background pigmentation, anterior, and posterior margins brown;
12 background pigmentation brown, anterior margin dark brown, posterior margin light brown;
12 background pigment, anterior and posterior margins brown to light brown;
12 background pigment, anterior and posterior margins brown to light brown;
12 background pigmentation light brown, anterior and posterior margins brown to light brown;

13 clothing setae short, densely scattered with small yellow spots at attachment points.
13 clothing setae short, densely scattered with small yellow spots at attachment points.
13 clothing setae short, densely scattered with small yellow spots at attachment points.

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

13 clothing setae short, densely scattered with small yellow spots at attachment points, a few dark, short, erect, setae sparely scattered posteriorly, some with tiny semicircular dark spots marking attachment points, these generally forming moderately spaced row near anterior margin.
13 clothing setae short, densely scattered with small yellow spots at attachment points.
13 clothing setae short, densely scattered with small yellow spots at attachment points.
13 clothing setae short, densely scattered with small yellow spots at attachment points, a few partially erect, short, dark setae interspersed among these.
13 clothing setae short, densely scattered with small yellow spots at attachment points.

14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 19).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 38).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, stripe width variable, generally widest posteriorly, tapering slightly anteriorly to posterior margin of anterior transverse furrow, some specimens with stripe narrowly constricted at this point, expanding laterally inside furrow, tapered gradually to anterior margin (Fig. 58).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe bowling pin-shaped (Fig. 77).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 95).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to posterior margin of anterior transverse furrow, then expanded laterally inside and above the furrow (Fig. 114).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, generally stripe widest posteriorly, tapered slightly anteriorly to anterior margin of anterior transverse furrow, then expanded laterally above furrow (Fig. 133).
14 Pronotal median longitudinal yellow stripe with small amounts of variable pigment along dorsal suture, stripe width variable, generally widest posteriorly, tapering slightly anteriorly to posterior border of anterior transverse furrow, some specimens with stripe narrowly constricted at this point, expanding laterally above anterior furrow to anterior margin (Fig. 152).

15 Mesonotum dark brown with variable areas of light pigment centrally and along sutures of notal plates.
15 Mesonotum dark brown with variable and irregular areas of light pigment centrally and along dorsal suture, appearing as continuation of pronotal median longitudinal stripe.
15 Mesonotum dark brown with variable and irregular areas of light pigment centrally and along sutures of notal plates.
15 Mesonotum dark brown with variable areas of light pigment centrally and along sutures of notal plates.
15 Mesonotum dark brown with thin, longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe.
15 Mesonotum dark brown with thin, longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe.
15 Mesonotum dark brown with variable longitudinal light stripe, appearing as continuation of pronotal median longitudinal stripe.
15 Mesonotum dark brown with variable and irregular areas of light pigment centrally and along sutures of notal plates.

16 Legs light brown to yellow with transverse, dark brown band covering above and below femur-tibia joints;
outside, lateral femur with densely scattered clear, short, thin clothing setae;
dark brown, tiny, erect setae broadly scattered, nearly same length as clothing setae;
without 1–2 hairless streaks;
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins.
16 Legs light brown to dark brown with transverse, dark brown band covering above and below femur-tibia joints,
outside, lateral femur with densely scattered, clear, short, thin clothing setae;
without dark brown, thin, erect setae;
1–2 variable length, thin hairless streaks on outside surface,
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins.
16 Legs light brown to dark brown, dark brown transverse band covering above and below femur-tibia joints, thin yellow-brown pigment area at femur-tibia joints muddled, difficult to discern,
outside, lateral femur with densely scattered clear, short, thin clothing setae;
without dark brown, thin, erect setae;
with 1–2 variable length, thin hairless streaks on outer surface;
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins.
16 Legs light brown to yellow with weak, transverse, brown band covering above and below femur-tibia joints, dark brown pigment usually forming variable dorsal, longitudinal stripes

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

on femur;
outside, lateral femur with densely scattered clear, short, thin clothing setae;
dark brown, tiny, erect setae broadly scattered, nearly same length as clothing setae;
with 1–2 variable length, thin hairless streaks on outer surface;
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins.
16 Legs brown with transverse, dark brown, almost black band covering anterior portion of tibia, thin yellow pigment at femur-tibia joints;
outside, lateral femur with densely scattered, clear, short, thin, clothing setae;
without dark brown, thin, erect setae;
without thin hairless streaks;
preserved specimens with femur light brown, brown to dark brown on dorsum, transverse banding on femur-tibia diffuse;
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior and inner, lateral margins.
16 Legs brown with transverse, dark brown, almost black band covering anterior portion of tibia, thin yellow pigment at femur-tibia joints;
outside, lateral femur with densely scattered, clear, short, thin, clothing setae;
without dark brown, thin, erect setae;
with 1–2 variable length, thin hairless streaks on outer surface;
tibia with dense clothing setae and scattered, erect, golden spines evenly distributed in moderately spaced longitudinal rows on posterior and inner, lateral margins;
distal portion of tibia with short, thin, raised carinae below transverse dark band;
16 Legs brown, with short, transverse dark brown, almost black band covering tibia-femur joint, femur with dark pigment continuing as thin dorsal stripe to base, thick yellow pigment at femur-tibia joint;
outside, lateral femur with densely scattered, clear, short, thin, clothing setae;
without dark brown, thin, erect setae;
with 1–2 variable length, thin hairless streaks on outer surface;
tibia with dense clothing setae and scattered, erect, golden spines evenly distributed in moderately spaced longitudinal rows along posterior margins.
16 Legs light brown to yellow, dark brown transverse band covering above and below femur-tibia joints, thin yellow pigment area at femur-tibia joints,
outside, lateral femur with dense, clear, short, clothing setae,
dark brown and clear, short, erect setae scattered;
with 1–2 variable length, thin hairless streaks on outer surface;
tibia with dense clothing setae and scattered, erect, golden spines sparse proximally, forming moderate, evenly spaced longitudinal rows along posterior margins.

17 Abdomen brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin;
17 Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin;
17 Abdomen dark brown to black with thick dark brown to black transverse bands along anterior margins of segments 6 or 7–9;
17 Abdomen brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin;
17 Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin;
17 Abdomen dark brown with thin dark brown to black transverse stripes along anterior margins, normally overlapped by preceding segment's posterior margin;
17 Abdomen dark brown without thin dark brown to black transverse stripes along anterior margins;
17 Abdomen light brown to brown with thick dark brown to black transverse bands along anterior margins of segments 2–9;

18 first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to yellow;
18 first two terga with variable-shaped unpigmented areas, hemitergal and subanal lobes light brown to dark brown;
18 first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to brown;
18 first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown to yellow;
18 first three terga with variable-shaped unpigmented areas, hemitergal and subanal lobes light brown to yellow;
18 first tergum with variable-shaped unpigmented areas, dorsal areas of terga 7–9, hemitergal and subanal lobes with some light brown to yellow pigment;
18 first tergum with variable-shaped unpigmented areas, hemitergal and subanal lobes yellow in dorsal view, contrasting sharply with darker cerci;
18 first tergum with variable-shaped unpigmented areas, apices of hemitergal and subanal lobes light brown;

19 dorsum entirely covered with dense, short, clear clothing setae becoming longer on posterior expanded segments;
19 dorsum entirely covered with dense, short, clear clothing setae not becoming longer on posterior, slightly expanded segments, except longer on hemitergal lobes;
19 dorsum entirely covered with dense, short, clear clothing setae, slightly longer on slightly expanded posterior segments and on hemitergal lobe apices;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

19 dorsum entirely covered with dense, short, clear clothing setae becoming longer on posterior expanded segments;
19 dorsum covered with variable setation, long, clear, moderately dense, partially erect, hair-like setae on segments 1–5;
long hair-like setae on segments 5–6 restricted to anterior 1/2, posterior 1/2 short, clear, clothing setae;
7th segment with short, clear, partially erect clothing setae;
segments 8–9 with short clothing setae anteriorly, longer at posterior margins of dorsally expanded humps;
19 dorsum entirely covered with long, clear, moderately dense, clothing setae;
posterior margin of 8th tergite with longer, partially erect clothing setae.
19 dorsum entirely covered with dense, short, clear to light brown, clothing setae, longer at mesoposterior areas of terga 8–9, those on 8 longest;
19 dorsum entirely covered with dense, short, clear clothing setae, slightly longer on segments 3–9, along posterior margins;

20 dorsolateral humps on terga 6–9 expanded into paired pin cushion-like swellings, those on 7th segment largest, sometimes extending beyond anterior margin of segment eight, covered with long, clear to golden, thin clothing or hair-like setae (Figs. 12–14).
20 dorsolateral humps on terga 6–9 small, hardly evident in dorsal view, posterolateral margins of 7th tergum slightly swollen laterally, not posteriorly, posterolateral swollen area of tergum 8 with narrow transverse patches of slightly longer, golden, hair-like setae (Figs. 32, 33).
20 dorsolateral humps on terga 6–9 moderate, evident in dorsal view, posterior and lateral margins of terga 7–8 slightly swollen, those on eight largest, dorsolateral swollen areas of terga 7–8 with dense patches of slightly longer, clear to golden clothing setae (Figs. 51, 52).
20 dorsolateral humps on terga 6–9 expanded into paired pin cushion-like swellings, those on 7th segment largest, sometimes extending beyond anterior margin of segment eight, covered with long, clear to golden, thin clothing or hair-like setae (Fig. 70, 71).
20 dorsolateral humps small, variable, restricted to terga 8–9, hardly evident in dorsal view;
posterolateral areas of 8th tergum slightly swollen dorsally, not laterally or posteriorly, swollen areas of tergum 8 with narrow transverse patches of slightly longer, clear, clothing setae posteriorly;
9th tergum with minutely swollen transverse lateral areas, with slightly longer clothing setae scattered posterior of hump to posterior margin (Figs. 89, 91).
20 dorsolateral humps small, variable, usually restricted to terga 7–8, visible in dorsal view;
posterolateral areas of 7th – 8th terga slightly swollen dorsally, rarely laterally, not posteriorly, swollen areas of 8th tergite largest, sometimes with thin transverse dorsal yellow marking near posterior margin;
narrow transverse patches of partially erect clothing setae along posterior margin of hump (Figs. 108, 109).
20 dorsolateral humps small, restricted to terga 8–9, visible in dorsal view, posterolateral areas slightly swollen dorsally, not laterally or posteriorly, swollen areas of 8th tergite largest;
9th tergite with variable transverse light area;
wide transverse patches of partially erect clothing setae cover dorsal areas of humps (Figs. 127, 128).
20 dorsolateral humps on terga 6–9 moderate, evident in dorsal view, posterior margins of terga 7–8 slightly swollen, those on eight largest, with dense patches of slightly longer, clear to golden clothing setae (Figs. 146, 148).

21 Sternal lobe large, located along mesoposterior margin, broadly rounded, with lighter, almost yellow pigment, surrounding areas dark brown, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe large, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with lighter brown or yellow pigment, the lightest along posterior margin, then blending anteriorly into surrounding darker pigment, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe small, short but well defined, located along mesoposterior margin of 7th sternite, broadly rounded, its posterior margin sometimes folded under, appearing absent except for small dark markings centrally, usually partially filled with light brown or yellow pigment with thin dark brown band along posterior margin.
21 Sternal lobe large, located along mesoposterior margin, broadly rounded, with lighter, almost yellow pigment, surrounding areas dark brown, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe moderate, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with lighter brown or yellow pigment, the lightest along posterior margin, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe moderate, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with lighter brown or yellow pigment, the lightest along posterior margin, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe large, located along mesoposterior margin of 7th sternite, broadly rounded, usually filled with yellow pigment, posterior margin not extending past posterolateral margins of 7th sternite.
21 Sternal lobe unusual, posteriorly not well defined, located slightly above mesoposterior margin of 7th sternite;
mesoposterior margin of lobe ending before reaching abdominal segment margin;
mesoposterior abdominal segment margin rounded, produced slightly below posterolateral margins, similar mesoposterior marginal protrusions sometimes present on sterna six and eight;

in other specimens, protrusions vestigial, without indication of lobe other than slight rounded, mesoposterior protrusion of anterior dark pigment band.

22 Hemitergal lobes in dorsal view of everted specimens with lobe apices directed medially and anteriorly, inner-posterior margins usually sharp, sometimes obtuse, but slightly angled (Fig. 13);
non-everted specimens with distal-most, anteriorly directed lobes generally in contact along entire inner-median margins, inner-posterior margins usually angulate (Figs. 12, 14);
connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Figs. 12, 14);
22 Hemitergal lobes in dorsal view with lobe apices directed medially and posteriorly, apical margins broadly rounded, connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 33);
22 Hemitergal lobes in dorsal view with lobe apices directed medially and slightly posterior, apical margins narrowly rounded, connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 52);
22 Hemitergal lobes in dorsal view of everted specimens with lobe apices directed medially and anteriorly, inner-posterior margins usually broadly rounded, appearing obtuse (Fig. 71);
non-everted specimens with distal-most, anteriorly directed lobes generally in contact mesoanteriorly at most, inner-posterior margins usually evenly curved;
connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 70, 71);
22 Hemitergal lobes in dorsal view with lobe apices directed medially and posteriorly, apical margins broadly rounded, connected anteriorly by small, hardly visible membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 89);
22 Hemitergal lobes in dorsal view with lobe apices directed medially and slightly posteriorly, apical margins broadly rounded, connected anteriorly by moderately large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 109);
22 Hemitergal lobes in dorsal view with lobe apices directed posteriorly, not medially or anteriorly, apical margins narrowly rounded to slightly pointed, connected anteriorly by tiny, thin, laterally extended membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 128);
22 Hemitergal lobes in dorsal view of with lobe apices directed medially and slightly posteriorly, apical margins narrowly rounded, connected anteriorly by large membranous area to mesoanterior wing-like internal basal anchor sclerites (Fig. 146);

23 20–34 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 12–14);
23 16–20 golden, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 32, 33);
23 18–38 light brown, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 51, 52);
23 26–42 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 70, 71);
23 10–20 light brown, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 89, 91);
23 38–42 reddish-brown, mostly long, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin (Figs. 108, 109);
23 14–20 golden brown, wide, mostly short, stout spinulae (sensilla basiconica) concentrated along mesoanterior margins of sclerites (Figs. 127, 128;
23 20–38 golden, mostly short, stout spinulae (sensilla basiconica) concentrated along anterior distal sclerite margin and membranous tissue near sclerite (Figs. 146, 148;

24 short, dark, scattered, erect setae and long, clear, moderately dense, fine setae concentrated along posterior and inner margins.
24 short, dark, erect setae scattered posteriorly on lobe apex continuing laterally and anteriorly, these interspersed within long, numerous, golden, hair-like setae concentrated along posterior margin of lobe apex.
24 short, dark, erect setae variable, when present, scattered posteriorly on lobe apex, these interspersed within variable length, clear, fine setae concentrated along posterior margin of lobe.
24 short, dark, scattered, erect setae and long, clear, moderately dense, fine setae concentrated along posterior and inner margins.
24 short, dark, erect setae scattered laterally on lobe, a few anteriorly, these interspersed within long, numerous, golden, hair-like setae concentrated along posterior margin of lobe apex.
24 short, dark, erect setae sparse on posterior membranous portion, these interspersed within long, numerous, golden, hair-like setae covering entire posterior areas;
10^{th} sternite dark brown.
24 short, dark, erect setae scattered over entire posterior portion of lobe, these interspersed within long, numerous, golden, hair-like setae covering entire posterior areas;
10^{th} sternite with small variable dark pattern.
24 short, dark, erect setae interspersed within mostly short, golden, fine setae, or all golden, fine setae scattered over entire posterior portion of lobe, usually continuing anteriorly, covering most of anterior membranous area.

25 Epiproct apex in lateral view with single, stout, light brown or golden, posterior and ventrally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 18, 26, 27);
25 Epiproct apex in lateral view with single, stout, posteriorly directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 34, 45, 46);
25 Epiproct apex in lateral view with single, stout, posterior and dorsally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 53, 64, 65);

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

25 Epiproct apex in lateral view with single, stout, dark brown, posterior and ventrally directed hook, its extension from epiproct less than epiproct width in lateral view (Figs. 72, 83, 84);
25 Epiproct apex in lateral view with single, stout, posteriorly and ventrally directed hook, its extension from epiproct about equal to epiproct width in lateral view (Figs. 90, 102, 103);
38 Epiproct apex modified in lateral view, with double, stout anteriorly and ventrally directed hooks, their anterior extension from epiproct less than epiproct width in lateral view (Figs. 110, 121, 122);
25 Epiproct apex modified in lateral view, with deep, internally sclerotized groove, not a hook (Figs. 129, 140, 141);
25 Epiproct apex modified in lateral view, mostly membranous, without sclerotized hook (Figs. 147, 159, 160);

26 posterior margin without pair of ventrally directed sclerotized hooks;
26 posterior margin with slightly sclerotized pair of short, ventrally directed hooks, their position from apex about 1/3 to 1/2 total epiproct length in lateral view;
26 posterior margin with moderately heavy sclerotized pair of long, ventrally directed hooks, their position from apex about 1/5 to 1/6 total length of epiproct length in lateral view;
26 posterior margin without pair of ventrally directed sclerotized hooks;
26 posterior margin without pair of short, ventrally directed hooks;
26 posterior margin with single, curved, long, lash-like, dorsally directed process, its position from apex about 1/3 total epiproct length in lateral view;
26 posterior margin with heavily sclerotized pair of long, basally broad, posteriorly directed hooks, their position from apex about 1/5 to 1/6 total epiproct length in lateral view;
26 posterior margin without pair of ventrally or posteriorly directed hooks;

27 in lateral view, under high magnification, anterior portion of epiproct with long, apically straight, narrow, moderately pointed, scale-like setae, lateral margins with deep apically angled serrations (Fig. 28);
27 in lateral view, under high magnification, anterior portion of epiproct with long, apically curved, moderately narrow, sharply tipped, scale-like setae, lateral margins with deep apically angled serrations (Fig. 47);
27 in lateral view, under high magnification, anterior portion of epiproct with long, apically tapered, sharply pointed, scale-like setae, lateral margins without deep serrations (Fig. 66);
27 in lateral view, under high magnification, anterior portion of epiproct with long, apically expanded, round tipped, scale-like setae, lateral margins without serrations (Fig. 85);
27 in lateral view, under high magnification, anterior portion of epiproct with long, apically irregular, wide, broadly round-tipped, scale-like setae, lateral margins without angled serrations (Fig. 104);
27 in lateral view, under high magnification, anterior portion of epiproct with long, apically irregular, wide, variably-tipped, scale-like setae, apical tip pointed, broad to narrowly bifurcate, or multiple serrated (Fig. 123);
27 in lateral view under high magnification, anterior portion of epiproct with long, apically curved or slightly expanded, bluntly tipped, scale-like setae, lateral margins with deep, angled serrations (Fig. 142);
27 in lateral view, under high magnification, anterior portion of epiproct with long, triangular, sharply pointed, scale-like setae, lateral margins without deep serrations (Fig. 161);

28 anterior support sclerite trifid in anterior view, lateral and median arms longer than base (Fig. 16), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 18, 26), median arm narrow, tapered to sharp pointed apex ending before reaching 1/2 length of entire epiproct (Fig. 16);
28 anterior support sclerite trifid in anterior view, lateral arms as long as or slightly longer than base (Fig. 37), median arm approximately 1/2 as long as base, lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 34, 45), median arm wide at base, tapered gradually to sharp pointed apex ending before reaching 1/2 length of entire epiproct (Fig. 37);
28 anterior support sclerite trifid in anterior view, lateral and median arms shorter than base (Fig. 56), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 53, 64, 65), median arm wide at base, tapering gradually to pointed apex, ending after surpassing 1/2 length of entire epiproct (Fig. 56);
28 anterior support sclerite trifid in anterior view, lateral arms longer than base (Fig. 75), median arm subequal, lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 72, 83, 84), median arm narrow, tapered to sharp pointed apex ending approximately at 1/2 length of entire epiproct (Fig. 75);
28 anterior support sclerite trifid in anterior view, lateral and median arms shorter than base (Fig. 93), lateral arms in lateral view curved anteriorly at apex, giving appearance of anterior hooks (Figs. 90, 102), median arm variable, tapered gradually to sharp pointed apex either ending before or after surpassing apices of lateral arms, usually ending just after surpassing 1/2 length of entire epiproct (Fig. 93);
28 anterior support sclerite modified in anterior view, median arm wide, attached to base normally,
lateral arms separated from median arm, extending dorsally to where they connect to ventral margins of double apical hooks (Figs. 112);
28 anterior support sclerite trifid in anterior view, lateral arms stout, longer than base (Fig. 131), in lateral view curved anteriorly at apex with apical, anterior expansions forming thin, hook-like processes (Figs. 129, 140, 141), median arm separated from lateral arms basally, its apically pointed dorsal portion as long as base, ending before 1/2 length of entire epiproct (Fig. 131);
28 anterior support sclerite trifid in anterior view, lateral arms longer and median arm shorter than base (Fig. 150), lateral arms in lateral view with apices curved smoothly to contour of anterior margin (Figs. 147, 159), median arm wide at base, tapering gradually to pointed apex, ending after surpassing 1/2 length of entire epiproct (Fig. 150);

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins subequal above hole to nearly 3/4 length of total epiproct, tapering to narrow distal portion joining inner, posterior margin of apical hook (Fig. 15).
29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portion, lateral margins tapering slightly, then expanding slightly, to join laterally at about 1/2 to 2/3 total epiproct length from base to pair of short, lightly sclerotized, ventrally directed hooks, support sclerite continuing dorsally, tapering again gradually to broad apical point, ending near base of apical hook (Fig. 36).
29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins mostly parallel, only slight rounded protrusion about 1/2 length of total epiproct, sclerite minutely expanded to meet and connect laterally to pair of long, ventrally directed hooks at about 1/2 to 2/3 total epiproct length from base, support sclerite continues dorsally, tapered gradually to broad apical point, ending near base of apical hook (Fig. 55).
29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins tapering gradually from base to approximately 1/2 length of total epiproct, margins subequal to nearly 3/4 total length from base, tapering gradually to narrow distal portion, joining inner, posterior margin of apical hook (Fig. 74).
29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portion, lateral margins approximately parallel for 3/4 length of epiproct from base, tapering gradually to narrow distal portion, joining inner posterior margin of apical hook (Fig. 92).
29 posterior support sclerite modified, stout, wide at base, extending dorsally and laterally, forming partially membranous plate with two apical, small, sclerotized dorsolateral margins that partially occlude posterior portions of lateral stylets,
base with irregular hole slightly more dorsal than normal,
dorsal portion of anterior support sclerite modified, projecting posteriorly and dorsally away from membranous epiproct, tabular sclerite curls posteriorly and anteriorly forming progressively smaller coil (Fig. 111).
29 posterior support sclerite single, stout, wide, lateral margins approximately parallel, with irregular-shaped hole near base below membranous epiproct portion, lateral margins expanding sharply to join laterally at slightly more than 3/4 total epiproct length from base, to pair of stout, heavily sclerotized, inwardly and posteriorly directed hooks, support sclerite continuing dorsally, margins parallel then tapering sharply, connecting to broad, apical, sclerotized groove (Fig. 130).
29 posterior support sclerite single, stout, long and tapered, with irregular-shaped hole at base below lateral membranous epiproct portions, lateral margins mostly parallel to about mid-length, tapering gradually to narrow tip at apex (Fig. 149).

30 Internal basal anchor in anterior view with wide base tapering gradually to nearly parallel where anterior keel-like sclerite connects, expanding laterally into short, rounded plates (Fig. 17);
30 Internal basal anchor in anterior view hour glass-shaped with wide base tapering gradually to where anterior keel-like sclerite connects, expanding laterally into long, rounded lateral plates (Fig. 35);
30 Internal basal anchor in anterior view with wide base tapering to where anterior keel-like sclerite connects, expanding gradually into small, pointed lateral plates (Fig. 53);
30 Internal basal anchor in anterior view with wide base tapering inwards at lower 1/4 length, gradual outwards taper to approximately dorsal 1/2 length where anterior keel-like sclerite connects, gradually expanding into small, pointed lateral plates (Fig. 73);
30 Internal basal anchor in anterior view almost hour glass-shaped with narrowly expanded base tapering gradually to where anterior keel-like sclerite connects, expanding laterally into tall, rounded, lateral plates (Fig. 94);
30 Internal basal anchor in anterior view with narrowly expanded base tapering gradually to where anterior keel-like sclerite connects, expanding laterally into small, pointed, lateral plates (Fig. 113);
30 Internal basal anchor in anterior view with narrowly expanded base tapering gradually to where anterior keel-like sclerite connects, expanding gradually into broadly triangular lateral plates (Fig. 132);
30 Internal basal anchor in anterior view with wide base tapering to where anterior keel-like sclerite connects, expanding gradually into large, broadly pointed lateral plates (Fig. 151);

31 large, wing-like triangular sclerites dorsal-most, directed posterolaterally, central notch absent.
31 small, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located, wide, rounded notch.
31 large, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located wide, truncated notch.
31 large, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located, narrow, elongated plate.
31 long, bent, wing-like triangular sclerites dorsal-most, directed posterolaterally from centrally located wide notch.
31 long, slightly curved, wing-like triangular sclerites dorsal-most, directed laterally from centrally located narrow notch.
31 long, wide, slightly curved, wing-like triangular sclerites dorsal-most, directed dorsally from centrally located wide notch.
31 large, wing-like triangular sclerites dorsal-most, broadly curved, directed posterolaterally from centrally located narrow notch.

32 Lateral stylets in lateral view with long, narrow base (Fig. 18);

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

32 Lateral stylets in lateral view with long, narrow base (Fig. 34);
32 Lateral stylets in lateral view with long, wide base (Fig. 53);
32 Lateral stylets in lateral view with long, narrow base (Fig. 72);
32 Lateral stylets in lateral view with long, narrow base (Fig. 90);
32 Lateral stylets in lateral view with long, narrow base (Fig. 110);
32 Lateral stylets in lateral view with long, wide base (Fig. 129);
32 Lateral stylets in lateral view with long, narrow base (Fig. 147);

33 expanded areas variable, at approximately 1/2 to 2/3 total length from base;
apical portion narrow at expanded region, margins mostly parallel, narrowly rounded tips;
33 expanded areas at nearly 2/3 total length from base, parts of expanded region lightly sclerotized, barely visible along inner and dorsal margins;
apical 1/3 narrow at expanded region, margins tapering gradually to narrowly rounded tips, angled margins minutely serrate;
33 expanded areas variable in shape and placement, usually with small posterior rounded tab curved interiorly and from 2/3 to 3/4 length of total epiproct from base;
apical portion wide, irregular-shaped, margins tapering abruptly to narrowly rounded tips, angled margins minutely serrate;
33 expanded areas variable, at nearly 2/3 total length from base;
apical 1/3 wide, irregular-shaped at expanded region, margins sub-triangulate, tapering to bluntly pointed tips;
33 expanded areas widely rounded at nearly 3/4 total length from base, parts of expanded region lightly sclerotized,
apical 1/4 wide, irregular-shaped at expanded region, margins parallel, then tapering gradually to narrowly rounded tips, posterior margin moderately serrate;
33 expanded areas widely rounded at nearly 3/4 total length from base,
apical 1/4 wide, irregular-shaped at expanded region, margins tapering gradually, curves posteriorly to sharply pointed tip;
33 expanded areas narrowly rounded at slightly more than 1/2 total length from base,
apical 1/2 narrow at expanded region, margins approximately parallel, curving slightly to broadly rounded tips;
33 expanded areas at approximately 3/4 length of total epiproct from base;
apical 1/4 wide, irregular-shaped at expanded region, margins tapering to broadly rounded tips;

34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 15, 29);
apical portions smoothly curved, apices directed slightly laterally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 36, 48);
apical portions smoothly curved, apices directed dorsally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 55, 67);
apical portions smoothly curved, apices directed slightly laterally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 74, 75);
apical portions irregularly curved, apices angulate, directed laterally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 92, 105);
apical portions smoothly curved, apices directed dorsally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 121, 136);
apical portions smoothly curved, apices directed slightly laterally.
34 in anterior or posterior view, stylets appearing about as wide as in lateral view (Figs. 130, 143);
apical portions smoothly curved, apices directed slightly laterally.
34 in anterior or posterior view, stylets appearing slightly wider than in lateral view (Figs. 149, 162);
apical portions smoothly curved, apices directed dorsally.

35 Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

35 Paragenital plates small, situated laterally on membranous tissue surrounding epiproct, completely hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates small, thin, situated laterally on membranous tissue surrounding epiproct, mostly hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates large, with distinct longitudinal carinae, situated laterally on membranous tissue surrounding epiproct, mostly hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.
35 Paragenital plates large, situated laterally on membranous tissue surrounding epiproct, partially hidden dorsally by hemitergal lobe, posteriorly by subanal lobe in non-everted specimens.

36 Subanal lobes rounded with dorsally and posteriorly directed lobe completely sclerotized outside, membranous inside, sclerotized plate light brown without membranous notch;
36 Subanal lobes rounded with posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate with long U-shaped membranous notch reaching approximately 1/3 length from apex in posterior view;
36 Subanal lobes rounded with dorsally and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate brown with wide U-shaped membranous notch reaching approximately 1/3 length of lobe from apex in posterior view;
36 Subanal lobes rounded with dorsally and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate light to dark brown with membranous notch broadly rounded along distal margin;
36 Subanal lobes rounded with dorsal and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate with wide U-shaped membranous notch beginning along mesal margins, reaching approximately 1/2 length from apex in posterior view;
36 Subanal lobes rounded with dorsal and posteriorly directed lobe, membranous along its dorsal and posterior margins, sclerotized plate with wide U-shaped membranous notch, reaching approximately 3/4 length from apex in posterior view;
36 Subanal lobes rounded with dorsal and posteriorly directed lobe not completely sclerotized outside, membranous inside, sclerotized plate covering approximately 1/2 length of entire lobe with wide U-shaped notch beginning along mesal margin, reaching 3/4 length from apex in posterior view;
36 Subanal lobes rounded with dorsally and posteriorly directed lobe not completely sclerotized outside, membranous inside, lightly sclerotized plate light brown, its variable dorsal margin broadly to narrowly pointed, ending before membranous round margin;

37 long, fine hair-like setae located centrally and along posterior margins of sclerotized plate.
37 long, fine hair-like setae on dorsal yellow portion, short, clothing setae on basal brown portion of sclerotized plate.
37 long, fine hair-like setae on posterior dorsal portion, becoming shorter on ventral portion.
37 long, fine hair-like setae scattered moderately over entire sclerotized plate, sometimes shorter setae on ventral portions.
37 long, fine hair-like setae covering entire plate.
37 long, fine hair-like setae covering entire plate.
37 long, fine hair-like setae covering entire plate.
37 long, fine hair-like setae on posterior dorsal portion, becoming shorter on ventral portion.

38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 21, 22);
tiny, clear, erect setae sparsely scattered mostly along posterior margin of lateral lobe;
two smaller lobes dorsally, close to distal margin, may not be fully everted, their inverted bases only visible (Fig. 21);
one wide, broadly rounded lobe projects slightly from distal margin.
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 40, 41);
tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes;
two smaller pairs of lobes dorsally and ventrally, close to distal margin (Figs. 40, 41).
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 59, 60);
tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes;
one wide dorsal subapical lobe located between lateral lobes, not surpassing bases of lateral lobes (Fig. 59);
one small ventral apical lobe located along posterior margin.
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral, apical margins (Figs. 78, 79);
tiny, clear, erect setae sparsely scattered over entire lateral lobe margins;
two smaller lobes dorsally, close to distal margin, may not be fully everted, their inverted bases only visible (Fig. 78);
ventral wide, broadly rounded lobe projects slightly from distal margin.
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 97, 98);

tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes;
two large lobes dorsally, set between, slightly below lateral lobes (Fig. 97);
two smaller lobes ventrally, between and slightly below lateral lobes, may not be fully everted, their inverted bases only visible (Fig. 98);
distal, broadly rounded lobe projects slightly from margin in ventral view.
38 Aedeagus membranous with pair of distinct lateral lobes slightly below dorsolateral apical margins (Figs. 108, 109);
two smaller lobes located and directed dorsally on aedeagus, situated between lateral lobes (Fig. 109);
tiny, clear, erect setae sparsely scattered over entire surface of small, dorsally directed lobes;
one wide, low, rounded knob located mesally and apically as seen in dorsal view.
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 135, 136);
tiny, clear, erect setae sparsely scattered over entire surface of lateral lobes;
two wide lobes dorsally, set between, slightly below, lateral lobes (Fig. 135);
two plate-like lobes ventrally, immediately below lateral lobes (Figs. 1A, 127), may not be fully everted in some specimens, their inverted bases only visible (Fig. 136), dorsal apex sometimes bearing globular, fixed extruded semen appearing as additional lobes (Figs. 1A, 127);
one low, moderately projected rounded knob, located mesally and apically as seen in dorsal view.
38 Aedeagus membranous with pair of distinct lateral lobes at dorsolateral apical margins (Figs. 154, 155);
tiny, clear, erect setae densely scattered over entire surface of lateral lobes, few scattered near mesal apex;
two small lobes dorsally, close to dorsoposterior, raised margin, may not be fully everted, their inverted bases only visible (Fig. 154);
two small lobes ventrally, between lateral lobes, may not be fully everted, their bases only visible (Fig. 155);
one large, mesally projected, rounded lobe, located apically as seen in dorsal or ventral views.

39 Cercal segments brown, 25–26 segments, basal-most not fully sclerotized;
39 Cercal segments brown, 21–25 segments, basal-most not fully sclerotized;
39 Cercal segments brown, generally darker along apical margins, 23–27 segments, basal-most not fully sclerotized;
39 Cercal segments brown, 24–27 segments, basal-most not fully sclerotized;
39 Cercal segments brown, 20–22 segments, basal-most not fully sclerotized;
39 Cercal segments brown, 20–24 segments, basal-most not fully sclerotized;
39 Cercal segments dark brown, 25–27 segments, basal-most not fully sclerotized;
39 Cercal segments light brown to brown, 30–32 segments, basal-most mostly sclerotized;

40 basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter distal segments;
40 basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter on distal segments;
40 basal 10–15 segments with slightly longer, golden, hair-like setae scattered, mostly at apical margins, these segments covered with short, dense, partially erect, golden setae, becoming less dense, slightly shorter, clear, clothing setae on remaining segments;
40 basal 5–10 segments completely covered with dense, long, golden, hair-like setae, longest on basal segments, becoming shorter distal segments;
40 basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments, becoming shorter and scattered on distal segments;
40 basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments, becoming shorter and scattered on distal segments;
40 basal 5–10 segments with densely scattered, long, golden, hair-like setae, longest and densest on basal segments; becoming shorter and scattered on distal segments;
40 basal 10–15 segments with slightly longer, golden, hair-like setae scattered, mostly at apical margins, these segments covered with short, dense, partially erect, golden setae, becoming less dense, slightly shorter, clear, clothing setae on remaining segments;

41 tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal segments;
41 tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal segments;
41 tiny, dark, erect, setae apparently absent;
41 tiny, dark, erect, setae dense at basal 5–8 segments, becoming sparsely scattered on distal segments;
41 tiny, dark, erect, setae sparse at basal 5–8 segments, becoming more dense on distal segments;
41 tiny, dark, erect, setae apparently absent;
41 short, dark, erect, setae apparently absent;
41 tiny, dark, erect, setae scattered on basal segments, less so, distally;

42 groups of 3–10 long, golden, stout setae project ventrally from mesoposterior margin;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

distal segments covered with short, dense, clear clothing setae.
42 groups of 3–6 long, golden, stout setae project posteroventrally from mesoposterior apical margin;
distal segments with short, dense, clear clothing setae.
42 groups of 3–6 long, golden, stout setae project ventrally from mesoposterior, apical margin.
42 groups of 3–10 long, golden, stout setae project ventrally from mesoposterior margin;
distal segments covered with short, dense, clear clothing setae.
42 groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin;
distal segments covered with short, dense, clear, partially erect clothing setae;
secondary, apical constrictions sometimes present on some distal segments.
42 groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin;
distal segments covered with short, dense, clear, partially erect clothing setae.
42 groups of 3–6 long, golden brown, stout setae project posteroventrally from mesoposterior apical margin;
distal segments covered with shorter, less dense, brown, partially erect clothing setae.
42 groups of 3–6 long, golden, stout setae project ventrally from mesoposterior apical margins;
distal segments with less dense, slightly shorter, clear, clothing setae.

Female. —
1 Macropterous.
1 Macropterous.
1 Macropterous.
1 Macropterous.
1 Macropterous.
1 Macropterous.
1 Macropterous.
1 Macropterous.

2 Length of forewings 15–18 mm; length of body 14–19 mm.
2 Length of forewings 15.5–17 mm; length of body 15–19 mm.
2 Length of forewings 18–22 mm; length of body 17–22 mm.
2 Length of forewings 17–19 mm; length of body 17–19 mm.
2 Length of forewings 17–18 mm; length of body 15–18 mm.
2 Length of forewings 16–18 mm; length of body 17–20 mm.
2 Length of forewings 16–18 mm; length of body 17–20 mm.
2 Length of forewings 20–22 mm; length of body 17–25 mm.

3 General body color, and head-pronotal pigmentation patterns similar to males.
3General body color, and head-pronotal pigmentation patterns similar to males.
3 General body color, and head-pronotal pigmentation patterns somewhat similar to males; wingpads larger than males.
3 General body color, and head-pronotal pigmentation patterns similar to males.
3 General body color generally lighter, and head-pronotal pigmentation patterns similar to males.
3 General body color generally lighter, and head-pronotal pigmentation patterns similar to males.
3 General body color and head-pronotal pigmentation patterns similar to males.
3 General body color, and head-pronotal pigmentation patterns somewhat similar to males; wingpads larger than males.

l.c. Subgenital plate broad at base, its width approximately 3/4 width of 8^{th} sternum,
produced from 1/4 to 3/4 length of 9^{th} sternum, broadly rounded posterior margin with deep, variable, mesoposterior notch, from U to V-shaped (Figs. 20, 30);
l. d. Subgenital plate broad at base, its width approximately 3/4 width of 8^{th} sternum,
produced from 1/3 to 2/3 length of 9^{th} sternum; broadly rounded posterior margin with variable mesoposterior characters (Figs. 39, 49):
1. mesoposterior margin of subgenital plate with small, slightly protruding nipple-like knob,
2. mesoposterior margin of subgenital plate with small, slightly rounded emargination,

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

3. mesoposterior margin of subgenital plate with a small, emarginated, slightly protruding double nipple-like knob, and
4. posterior margin of subgenital plate entire;
l.e. Subgenital plate broad at base, its width from 2/3 to 3/4 width of 8th sternum;
produced from 1/4 to 1/2 length of 9th sternum;
posterior margin nearly quadrate or truncate with variable mesoposterior characters (Figs. 57, 68):
1. mesoposterior margin of subgenital plate with small, slightly protruding nipple-like knob,
2. mesoposterior margin of subgenital plate with small, slightly rounded emargination,
3. mesoposterior margin of subgenital plate with small, emarginated, slightly protruding double nipple-like knob, and
4. posterior margin of subgenital plate entire or sometimes weakly and broadly emarginated its entire width;
l.f. Subgenital plate broad at base, its width approximately 3/4 width of 8th sternum,
produced from 1/4 to 3/4 length of 9th sternum, broadly rounded posterior margin with variable, deep, mesoposterior notch, from U to V-shaped (Figs. 76, 87);
l.h. Subgenital plate moderately broad at base, its width usually less than 3/4 width of 8th sternum,
produced from 1/2 to 3/4 length of 9th sternum; broadly rounded posterior margin (Figs. 96, 106);
l.o. Subgenital plate moderately broad at base, its width usually less than 3/4 width of 8th sternum,
produced from 1/2 to 2/3 length of 9th sternum, broadly rounded posterior margin with variable mesoposterior emargination from broad and shallow to narrow and moderately deep (Figs. 111, 124);
l.v. Subgenital plate broad at base, its width usually greater than 3/4 width of 8th sternum,
produced from 3/4 to entire length of 9th sternum; broadly rounded posterior margin with variable mesoposterior characters (Figs. 134, 144):
1. mesoposterior margin of subgenital plate with short, almost vestigial, wide protrusion,
2. mesoposterior margin of subgenital plate with short, almost vestigial, narrow to wide, emarginated protrusion,
3. posterior margin of subgenital plate entire;
l.z. Subgenital plate moderately broad at base, its width approximately 2/3 width of 8th sternum, a few sometimes wider;
produced from 1/4 to 1/3 length of 9th sternum;
posterior margin nearly quadrate or truncate with variable mesoposterior characters (Figs. 153, 163):
1. mesoposterior margin of subgenital plate with small to moderate, rounded, protruding nipple-like knob,
2. mesoposterior margin of subgenital plate with small to moderate, emarginated, protruding double nipple-like knob,
3. mesoposterior margin of subgenital plate nearly entire with vestigial emarginated double-protrusions barely visible;

5 dark pigment mostly anterior and lateral with two smaller dark markings on plate, below mesally-angled posterior margins of abdomen, some females have a slightly darkened posterior margin including mesoposterior emargination.
5 dark pigmentation mostly anterior and lateral with two, smaller dark brown markings on plate, below mesally-angled posterior margins of abdomen, these markings enclosed by larger light brown markings.
5 dark pigmentation variable, mostly anterior and lateral with two small dark markings on plate, below mesally-angled posterior margins of the abdomen, some specimens have the entire posterior margin lightly pigmented.
5 dark pigment patterns variable, from almost entirely brown to almost entirely yellow, consistently with two smaller dark markings on plate, below mesally-angled posterior margins of abdomen.
5 dark pigmentation mostly anterior and lateral with two, smaller dark brown markings on plate, located along anterolateral margins of plate, below mesally-angled posterior margins of abdomen, these markings enclosed by larger light and dark brown markings;
mesally located, longitudinal yellow stripe variable, not always connected to posterior light margin.
5 dark pigmentation variable, from covering entire plate to patterned, with most dark pigment anteriorly and laterally with posterior margin light;
two variable, large, darker markings located anterolaterally on plate, usually connected to anterior segment by two thick, brown longitudinal bands.
5 dark pigmentation variable, from covering entire plate to patterned, sometimes with two, small, rounded light markings on plate, below mesally angled, posterior margins of abdomen, these markings enclosed by dark pigment posteriorly, connected to two, wide, light brown to yellow, longitudinal bands on anterior portion of segment;
5 dark pigmentation variable, usually along posterior margin, sometimes restricted to mesoposterior margin, laterally with two, small, brown markings on plate, below mesally angled posterior margins of abdomen, and variable pair of thin to wide longitudinal dark bands anteriorly on segment.

Nymph. —
1 General body color light brown to yellow with light and dark markings (Fig. 11).
1 General body color light brown to yellow with light and dark markings (Fig. 31).
1 General body color dark brown to light brown with light and dark markings (Fig. 50).

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

1 General body color brown with light and dark markings (Fig. 69).
1 General body color light brown with light and dark markings (Fig. 88).
1 General body color light brown with light and dark markings (Fig. 107).
1 General body color yellow with light and dark markings, yellow fading to cream when preserved (Fig. 126).
1 General body color brown to light brown with light and dark markings (Fig. 145).

2 Antennae light brown almost golden;
2 Antennae light tan almost yellow;
2 Antennae light brown almost golden;
2 Antennae light brown;
2 Antennae golden almost yellow;
2 Antennae golden almost yellow;
2 Antennae yellow to cream;
2 Antennae golden to light brown;

3 with short, erect, golden peg-like setae arranged as whorls around apical margins, sometimes a few on dorsal surface of first segment;
3 with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segments 1–3;
3 with short, erect, stout, golden peg-like setae arranged as apical whorls on segments 1–2, a few scattered on their dorsal surfaces, remaining segments with smaller, erect, golden peg-like setae in apical whorls;
3 with short, erect, golden peg-like setae arranged as whorls around apical margins, sometimes a few on dorsal surface of first segment;
3 with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segment 1;
3 with short, erect, golden peg-like setae arranged as whorls around apical margins, few scattered on dorsal surface of segment 1;
3 with short, erect, golden peg-like setae arranged as whorls around apical margins, segment one with scattered, long, dark clothing setae, these fading to clear when preserved;
3 with short, erect, stout, golden peg-like setae arranged as apical whorls on segments 1–2, a few scattered on dorsal surface of segment one, remaining segments with smaller, erect, golden peg-like setae in apical whorls;

4 usually with short sparse row of long, fine, clear, silky setae beginning on segment two, ending on segment 7–8;
4 usually with long sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 17–18;
4 usually with long sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 12–13;
4 usually with short sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 9–10;
4 usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 18–20;
4 usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 13–15;
4 usually with long, sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 17–19;
4 usually with long sparse row of long, fine, clear, silky setae beginning on segment three, ending on segment 15–22;

5 short, clear, intersegmental clothing setae sparsely scattered on segment one; minute, erect setae scattered on segment two.
5 short, clear, intersegmental setae apparently absent.
5 long, golden, intersegmental clothing setae on segment one.
5 short, clear, intersegmental clothing setae scattered on segment one; minute, erect setae scattered on segment two.
5 short, clear, intersegmental setae apparently absent.
5 short, clear, intersegmental setae apparently absent.
5 short, clear, intersegmental setae apparently absent.
5 long, golden, intersegmental clothing setae on segment 1–2, with several scattered, short, fine, clear, erect setae; .

6 Dorsum of head with contrasting pigment pattern; fine, short, clear, clothing setae sparsely scattered;
6 Dorsum of head with contrasting pigment pattern; fine, long, dark clothing setae densely scattered;
6 Dorsum of head with contrasting pigment pattern; fine short, clear clothing setae sparsely scattered;
6 Dorsum of head with or without contrasting pigment pattern, sometimes mostly brown to dark brown; fine, short, clear, clothing setae usually sparsely scattered to absent;
6 Dorsum of head with contrasting pigment pattern; fine, short, golden clothing setae sparsely scattered;
6 Dorsum of head with contrasting pigment pattern; fine, short, clear, clothing setae sparse;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

6 Dorsum of head with contrasting dark pigment pattern when live or recently preserved, becoming faded over time to light tan patterns mostly on posterior half; long dark clothing setae scattered mostly over pigmented areas;
6 Dorsum of head with contrasting pigment pattern; fine short, golden, clothing setae sparsely scattered;

7 light colored narrow band forming M-pattern between antennal bases and median ocellus;
7 light colored narrow band forming M-pattern between antennal bases and median ocellus open mesoanteriorly;
7 light colored narrow band forming M-pattern between antennal bases and median ocellus often open mesoanteriorly in preserved specimens, enclosed when recently preserved;
7 when present, light colored narrow band forming M-pattern between antennal bases and median ocellus, sometimes all brown;
7 light colored wide band forming M-pattern between antennal bases and median ocellus;
7 light colored narrow band forming M-pattern between antennal bases and median ocellus;
7 light colored narrow band forming M-pattern between antennal bases and median ocellus partially enclosed with dark pigment, its margins indicated by presence of long, dark moderately scattered, clothing setae enclosing pattern;
7 light colored narrow band forming M-pattern between antennal bases and median ocellus usually open mesoanteriorly;

8 anterior transverse brown band thick, completely enclosing M-pattern anteriorly;
8 anterior transverse brown band reduced to two short, thin, anteriorly curved bands beginning along anterolateral margins, incompletely enclosing M-pattern anteriorly;
8 anterior transverse brown band thick, occasionally enclosing M-pattern anteriorly, usually faded, open mesally on preserved specimens;
8 anterior transverse brown band thick, completely enclosing M-pattern anteriorly;
8 anterior transverse brown band variable, usually thin, curved posteriorly at lateral margins, completely enclosing M-pattern anteriorly;
8 anterior transverse brown band variable, usually thick, completely enclosing M-pattern anteriorly, becoming light brown or speckled with small yellow blotches along anterior margin;
8 anterior transverse brown band reduced, narrow, following contour of anterior M-pattern margin, usually faded on preserved specimens;
8 anterior transverse brown band thick laterally, faded, mostly open mesally, incompletely enclosing M-pattern anteriorly;

9 anterior margin with narrow transverse light band, brown area below, enclosing M-pattern with two small transversely flattened, thin, light areas above anterior-most portions of M-pattern;
9 anterior margin usually with broad transverse light band, generally extending mesoposteriorly to median ocellus, sometimes this area with faded, light brown pigment, brown bands below partially enclosing M-pattern without two light areas;
9 anterior margin with narrow transverse light band, variable brown area below, enclosing M-pattern with two small transversely flattened light areas above anterior-most portions of M-pattern, light transverse band sometimes extending posteriorly to median ocellus;
9 anterior margin with narrow transverse light band, brown area below, enclosing M-pattern with two small transversely flattened light areas above anterior-most portions of M-pattern;
9 anterior margin usually with narrow, laterally curved, transverse light band, brown area below enclosing M-pattern without two light areas, sometimes open anteriorly;
9 anterior margin usually with narrow, transverse light band, brown area below enclosing M-pattern without two small, transversely flattened light areas above anterior-most portions of M-pattern;
9 anterior margin largely yellow to unpigmented, 4 small, irregular shaped dark markings mesoanteriorly between antennal bases and labrum, brown band below without two light areas;
9 anterior margin with narrow transverse light band, generally extending mesoposteriorly to median ocellus, brown areas below variable, usually with two wide, transversely flattened light areas above anterior-most portions of M-pattern, sometimes open anteriorly;

10 two large, sometimes boot-shaped dark markings on anterolateral margins between antennal bases and labrum;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum, sometimes faded;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum, sometimes faded;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum, all six mostly faded in preserved material;
10 two small, irregular-shaped dark markings on anterolateral margins between antennal bases and labrum;

11 labrum with two semicircular dark markings along anterior margin;
11 labrum with two semicircular dark markings along anterior margin;
11 labrum with two, small, semicircular dark markings along anterior margin;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

11 labrum with two semicircular dark markings along anterior margin, two larger, faint, semicircular dark markings along posterior margin, some specimens with markings diffuse, narrowly connected;
11 labrum with two, small, semicircular dark markings along anterior margin;
11 labrum with two, small, semicircular dark markings along anterior margin;
11 labrum usually yellow to unpigmented, covered with long, dark clothing setae;
11 labrum with two, small, semicircular dark markings along anterior margin;

12 variable, flatly rounded, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern;
12 variable, flatly rounded, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern diffuse, open posteriorly and laterally;
12 variable, flatly rounded, curved, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern;
12 variable, flatly rounded, thin, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern;
12 variable, flatly rounded light areas absent;
12 variable, flatly rounded, sometimes broadly U-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern, these sometimes partially connected to
12 variable, flatly rounded, light areas absent;
12 variable, flatly rounded, curved, irregular-shaped light areas between inner margin of eyes, lateral ocelli, and posterior margin of M-pattern;

13 small, triangular-shaped light areas along outer lateral margins of lateral ocelli;
13 large, irregular-shaped light areas along outer margins and above lateral ocelli, continuing laterally, almost to bases of antennae,
13 small, triangular-shaped light areas along outer lateral margins of lateral ocelli;
13 small, triangular-shaped light areas along outer lateral margins of lateral ocelli;
13 large, tall, triangular-shaped light areas along outer margins of lateral ocelli, continuing laterally to antennal bases;
13 variable, small, triangular light areas along outer margins of lateral ocelli, sometimes large;
13 large, nearly triangular light areas above lateral ocelli, extending to median ocellus, laterally to inner margin of eye, anterior margins enclosed by thin, irregular-shaped, transverse brown band below M-pattern, this extending to anterior, inner margin of eyes;
13 variable, usually small, triangular-shaped light areas along outer lateral margins of lateral ocelli;

14 recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows.
14 recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows.
14 recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows.
14 recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows extending posteriorly from below epicranial arm sutures to inner occipital spinule rows.
14 recently preserved specimens with long, clear, silky setae in two, moderately dense, irregular-shaped patches on either side of epicranial stem suture, when present, extending from mesal patches to inner margin of eyes in irregular, moderately spaced rows, points of attachment marked by tiny yellow spots.
14 recently preserved specimens with long, clear, silky setae in two, sparse, irregular-shaped patches on either side of epicranial stem suture, reaching anterolaterally to inner margin of eye in widely spaced irregular row and posteriorly to mesal end of occipital spinulae row, points of attachment marked by tiny yellow spots.
14 recently preserved specimens with few, long, clear, silky setae in two, irregular, sparse patches near mesal portions of occipital spinule row.
14 recently preserved specimens with long, clear, silky setae in two sparse, irregular, mesal longitudinal rows with sparsely scattered, short, thin, erect setae interspersed, extending posteriorly from below epicranial arm sutures to inner occipital spinule rows.

15 Interocular area brown, similar to adjacent areas;
15 Interocular area brown, sometimes with variable, mesoposterior light brown marking extending posteriorly from below anterior ocellus to epicranial intersection;
15 Interocular area brown, similar to adjacent areas;
15 Interocular area brown, sometimes with variable, mesoposterior light brown marking extending posteriorly from below anterior ocellus to epicranial intersection;
15 Interocular area not completely brown, usually with variable, longitudinally narrow, oval-shaped yellow area in center;
15 Interocular area brown, similar to adjacent areas;
15 Interocular area brown, partially faded when preserved;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

15 Interocular area variable, usually brown, similar to adjacent areas anteriorly, posteriorly with variable mesoposterior faded area, sometimes extending posteriorly to epicranial suture intersection;

16 post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction.
16 post ocular and occipital spinule rows thin with many peg-like spinulae, longer, stout, spine absent in occipital row near post ocular row junction;
occipital spinule row sometimes interrupted by small gap.
16 post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction.
16 post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction.
16 post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction, another at mesal end of occipital row;
16 post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction, another at mesal end of occipital row;
16 post ocular and occipital spinule rows thin with many peg-like spinulae, usually with one longer spine in occipital row near post ocular row junction.
16 post ocular and occipital spinule rows thick with numerous peg-like spinulae, usually with one longer, stout, spine in occipital row near post ocular row junction, sometimes interrupted.

17 Lacinia with 1 axilary seta, 18–21 marginal setae below subapical tooth, 12–16 submarginal setae, scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 18–20 marginal setae below subapical tooth, 10–13 submarginal setae, scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 18–19 marginal setae below subapical tooth, 13–15 submarginal setae, scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 19–24 marginal setae below subapical tooth, 11–13 submarginal setae, scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 16–20 marginal setae below subapical tooth, 10–11 submarginal setae, scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 15–17 marginal setae below subapical tooth, 3–5 submarginal setae sparsely scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 15–18 marginal setae below subapical tooth, 9–11 submarginal setae sparsely scattered from below apical tooth downwards to base.
17 Lacinia with 1 axilary seta, 18–24 marginal setae below subapical tooth, 11–17 submarginal setae, scattered from below apical tooth downwards to base.

18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp variable, usually short indistinct row of small, vestigial denticles, occasionally distinct row of large, sharp denticles reaching about 1/2 length of inner margin (Fig. 3).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp with short, indistinct row of small denticles reaching about 1/2 length of cusp (Fig. 4).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp variable, usually with long distinct row of large denticles usually extending beyond 1/2 length of cusp, occasionally large denticles absent on one or both mandibles, or small, indistinct denticles restricted to approximately basal 1/2 of cusp on one or both mandibles (Fig. 5).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp variable, usually short indistinct row of small, vestigial denticles, occasionally distinct row of large, sharp denticles reaching about 1/2 length of inner margin (Fig. 6).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually reaching beyond 1/2 length of cusp of one or both mandibles (Fig. 7).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp with short, indistinct row of small, vestigial denticles sometimes reaching beyond 1/2 length of cusp of one or both mandibles (Fig. 8).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually extending beyond 1/2 length of cusp of one or both mandibles (Fig. 9).
18 Left and right mandible under high magnification with ventral basal margin of distal-most cusp with long, distinct row of large denticles usually extending beyond 1/2 length of cusp (Fig. 10) (Baumann 1973).

19 Submental gills at least 2x as long as width at base.
19 Submental gills approximately 2x as long as width at base.
19 Submental gills at least 2x as long as width at base.
19 Submental gills at least 2x as long as width at base.
19 Submental gills at least 2x as long as width at base.
19 Submental gills short, at most 2x as long as width at base.
19 Submental gills at least 2x as long as width at base.
19 Submental gills at least 2x as long as width at base.

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

20 Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs;
20 Pronotum mostly light brown dorsally and laterally with variably patterned central area light brown, tan or yellow;
20 Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs;
20 Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs;
20 Pronotum brown laterally with variable-shaped, central, light and dark markings;
20 Pronotum brown laterally with variable-shaped, central, light and dark markings;
20 Pronotum mostly yellow to unpigmented with variable-shaped, central, light and dark markings;
long dark, clothing setae moderately dense, covering mostly pigmented areas;
20 Pronotum mostly brown laterally with variable light linear patterns clustered mesally on pronotal discs;

21 anterior transverse furrow thick, dark brown, almost black anteriorly, anterior margin light brown to brown;
posterior transverse furrow thin, medium to dark brown, almost black posteriorly;
posterior margin light brown to brown, light lateral margins;
central pronotum distinctly patterned with two, nearly parallel brown bands on each side of light colored dorsal suture, extending posteriorly almost entire length of discs;
light colored, variable-shaped, curved, light stripes radiate from anteromesal to posterolateral areas, remainder mostly brown;
21 anterior transverse furrow thick, dark brown, almost black, anterior margin brown;
posterior transverse furrow thin, dark brown, almost black, tapering to narrow mesal points;
posterior margin brown, light lateral margins;
central area of pronotum distinctly patterned with two oppositely curved, narrow, light brown bands on each side of dorsal suture, extending posteriorly, almost entire length of discs, these mesal longitudinal bands fade to light tan or yellow in older specimens;
a second, variable-shaped light brown band positioned between mesal longitudinal band and about 1/2 width of disc, rarely remains intact after 1-year in alcohol;
irregular, variable-shaped network of light brown bands laterally, these variously joined to lateral, posterior borders of anterior furrows, sometimes beginning below posterior border markings, connecting posteriorly to irregular-shaped, light brown markings above posterior furrow;
21 anterior and posterior transverse furrows filled with medium to dark brown;
anterior and posterior margins usually with similar pigment, lateral margins light;
central pronotum usually distinctly patterned with two irregular-shaped, nearly parallel brown bands on each side of mostly light colored dorsal suture, extending almost entire length of discs, these bands usually connected centrally above and below an irregular-shaped light area posteriorly, light area faded in alcohol;
light colored, variable-shaped, curved, longitudinal light stripes longest and continuous near mesal longitudinal brown bands, other variable light areas usually small, rounded, concentrated mesally, remainder of pronotum mostly brown;
21 anterior transverse furrow thick, dark brown, almost black anteriorly, anterior margin light brown to brown;
posterior transverse furrow thin mesally, medium to dark brown, almost black anteriorly;
posterior margin brown, light lateral margins;
central pronotum indistinctly patterned with two, irregular-shaped, curved brown bands on each side of mostly light colored dorsal suture, extending almost entire length of discs, these bands usually connected centrally more than once, thus obscuring their distinctive shape, becoming more pronounced in older preserved specimens;
light colored, variable-shaped, curved, light stripes radiate from anteromesal to posterolateral areas, remainder of pronotum mostly brown;
21 anterior transverse furrow thick, dark brown, anterior margin brown to dark brown;
posterior furrow thin, dark brown, almost black posteriorly;
posterior margin brown, light lateral margins;
central area of pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to light brown in preserved specimens;
light colored bands, loosely assembled from smaller, curved, irregular-shaped segments directed posterolaterally, ending near mid-disc, enclosed by diffuse light brown;
posterior half of discs with areas of small, curved, irregular-shaped light bands, concentrated laterally below light angled bands and mesally below brown longitudinal bands; thin remaining lateral areas brown;
21 anterior transverse furrow thick, dark brown;
posterior transverse furrow thin, dark brown, almost black on posterior border;
anterior and posterior margins brown, lateral margins light;
central area of pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to light brown in preserved specimens;
variable, diffuse, light brown bands formed from smaller, curved, irregular-shaped segments radiate outwards, posterolaterally on central areas of each disc, enclosed by diffuse light

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

brown;
lateral and posterior areas of discs with variable-shaped, elongate, light stripes, remaining pronotum with various brown and light brown areas, on preserved specimens light colored stripes connected, additional stripe continuing towards anterior mesal area, forming irregular trapezoid shaped band over center of pronotum;
21 anterior transverse furrow thick, dark brown, anterior margin light to dark brown;
dark to light brown short, broadly rounded markings connected to posterolateral, anterior furrow borders;
posterior furrow variable, generally thick with thin section near dorsal suture curving posteriorly, filled with dark brown;
posterior margin light brown, lateral margins light;
dark to light brown variable, rounded markings connected to anterolateral and mesoanterior borders of posterior furrow;
central area of pronotum indistinctly patterned with two oppositely curved, narrow brown bands on each side of light colored dorsal suture, extending posteriorly to about basal 2/3 length of discs, these mesal longitudinal bands fade to speckled light tan in preserved specimens and are covered with long, dark, clothing setae;
one long, distinctly curved, longitudinal light stripe on outer lateral margins of median dark bands, followed by three, indistinct, loosely assembled light bands, formed from smaller, curved, irregular shaped segments, these directed posterolaterally, ending near mid-disc, enclosed by diffuse, light tan;
long, lateral, dark bands begin narrowly below lateral portions of anterior furrows, expanding posteriorly at posterior corners of discs;
21 anterior and posterior transverse furrows filled with medium to dark brown, anterior and posterior margins usually with similar pigment, lateral margins light;
central pronotum distinctly patterned with two oppositely curved, narrow brown bands on each side of partially light colored dorsal suture, extending posteriorly to almost entire length of discs, these bands join mesally for most their length;
dark and light brown bands radiate from mesoanterior to posterolateral areas, usually enclosed by light tan or light brown, these brown bands bordered by variable areas of light, rounded areas, remainder of pronotum mostly brown;

22 anterior and posterior margins with row of stout peg-like setae, sometimes with 1–4 longer setae near corners, lateral margin setae usually smaller, sometimes interrupted or absent near mid-length;
posterior margin peg-like setae with long, stout, erect setae scattered, long, fine, silky setae usually near dorsal suture;
22 anterolateral, lateral, and posterior margins with continuous, similarly sized, stout, peg-like setae;
22 margins with continuous, approximately similar sized, stout, peg-like setae;
22 anterior and lateral margins with row of stout peg-like setae, sometimes with 1–4 longer setae near corners, lateral margin setae usually similar to anterior, not interrupted near mid-length;
posterior margin peg-like setae generally becoming long, stout, erect setae, long fine, silky setae near dorsal suture;
22 anterior and posterior margins with variable setation, short, stout, peg-like setae interspersed with long, moderately stout, golden setae, lateral margins with only short, peg-like setae;
22 pronotal marginal setae variable, long silky setae mesally at anterior and posterior margins near dorsal suture;
anterior and posterior setae becoming long, stout, erect, golden setae with short, peg-like setae interspersed, continuing to lateral margins, sometimes with 1–4 longer setae near corners;
lateral margins with variable setation, from all short peg-like to interspersed with long, erect setae;
22 anterior and lateral margins with short, stout, peg-like setae, posterior margin with peg-like setae becoming longer mesally;
22 anterior and lateral margins with continuous, short, stout, peg-like setae; posterior margin with peg-like setae mixed with longer, golden, stout, erect setae;

23 pronotum covered with moderately sparse, short, clear, clothing setae.
23 pronotum covered with moderately dense, long, dark, clothing setae.
23 pronotum covered with moderately dense, short, clear, clothing setae.
23 pronotum covered with moderately sparse, short, clear, clothing setae.
23 pronotum covered with short, densely scattered, thin, dark clothing setae, these fading to gold or clear in preserved material.
23 pronotum covered with densely scattered, short, thin, clear clothing setae.
23 pronotum covered with long, moderately dense, dark clothing setae.
23 pronotum covered with moderately dense, short, clear, clothing setae.

24 Meso-Metanota light brown, usually a large pair of mesoanterior light oval areas on each disc, sometimes single, tear-drop shaped, with thin longitudinal dark band bisecting oval areas faded or absent in preserved specimens;
long, thin, curved, posteriorly widened, light areas mesally, near dorsal suture, between mesoanterior light areas;
variable heart-shaped light area along posterior half of dorsal suture.
24 Meso-Metanota light brown, usually with three pairs of mesoanterior, light, oval areas distinct;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

in preserved specimens, thin brown bands enclosing these areas fade, leaving golden spinulae and dark clothing setae to indicate their original margins;
another longer light area positioned below the three light oval areas, extending anterolaterally, meeting anterior, thick, dark brown transverse band;
wide heart-shaped light area along posterior half of dorsal suture open posteriorly, or partially closed with variable pigment in some;
wide, brown band or bands begin abruptly in mesolateral area of wing pad, continue on mesal posterior angles, reaching the posterior angled margin of wing pad.
24 Meso-Metanota mostly brown, usually mesoanterior light oval areas with variable thin brown bands bisecting oval areas faded or absent in preserved specimens, leaving large tear-drop shaped light areas as in *I. zionensis*;
long, thin, curved, posteriorly widened, light areas sometimes filled with dark pigment, appearing as row of irregular-shaped light spots, these fading, coalescing over time into one long band between mesoanterior light areas;
variable hour glass shaped light area along mesoposterior portion of dorsal suture can also be heart-shaped or rounded on meso-metanotum.
24 Meso-Metanota light brown, usually a large pair of mesoanterior light oval areas, sometimes single, tear-drop shaped, with thin longitudinal dark band bisecting oval areas faded or absent in preserved specimens;
long, thin, curved, posteriorly widened, light areas mesally, near dorsal suture, between mesoanterior light areas;
variable heart-shaped light area along posterior half of dorsal suture.
24 Meso-Metanota light brown, usually with two pairs of mesoanterior, light, oval areas indistinct, separated by thin light brown bands;
preserved specimens with thin brown band separating these areas faded, leaving dark clothing setae to indicate their original margins;
two long, curved light areas border mesoanterior, light oval-areas along their inner, posterior and outer margins;
heart-shaped light area along posterior half of dorsal suture absent;
anterior and posterior margins marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly bowl-shaped;
dark triangular bands adjacent to posterior bowl shaped markings;
24 Meso-Metanota light brown, usually with one pair of mesoanterior, light, oval areas indistinct, usually partially filled with light brown;
two long, curved, posteriorly widened, light areas border larger, light, oval areas along mesoposterior inner, margins;
a central pair of long, wide, anteriorly curved light bands positioned laterally, posterior to mesoanterior oval areas;
posterior heart-shaped light areas absent;
anterior and posterior margins marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly bowl-shaped;
faded brown triangular-shaped bands adjacent to posterior bowl-shaped markings present or absent;
24 Meso-Metanota yellow to cream when preserved, usually with two pairs of mesoanterior, light oval areas indistinctly separated by thin, light brown to tan bands;
a short thin pair centrally, along dorsal suture, and a large, thick, light area lateral of mesoanterior pair;
posteriorly, with a wide, short, light oval area near dorsal suture, separated from large, thick light area laterally with thin light brown to tan stripe;
posterior heart-shaped area absent;
anterior and posterior margins marked with distinct brown, irregular bands, anteriorly almost bird-shaped, posteriorly, bowl-shaped, open mesoposteriorly;
brown, triangular-shaped bands adjacent to posterior bowl-shaped markings faded.
24 Meso-Metanota partially brown usually mesoanterior light oval areas filled partially with light brown or tan, anterior and inner lateral, thin, dark pigment borders with short, stout setae, sometimes faded in alcohol;
long, thin, curved, posteriorly widened, light areas with lateral dark margins poorly defined in preserved material;
variable hour glass-shaped light area along mesoposterior margins, usually smaller on metanotum.

25 Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–9, segment one all brown except small, rounded, light area at mesoposterior margin, 10th tergum either with band as above or expanded posteriorly, following the contour of posterior margin, then cutting sharp anteriorly at lateral margins;
25 Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–10, segment one usually all brown except small, rounded, light area at mesoposterior margin, 10th tergum usually similar to 9th ;
25 Abdominal terga usually with indistinct, broad, dark, anterior transverse bands on segments 3–7, segment 1–2 all brown, 8–10 with variable mesoposterior light areas;
preserved specimens sometimes with anterior dark bands on all segments except first;
25 Abdominal terga with distinct, dark, anterior, transverse bands on segments 2–8, segment one all brown except small, rounded, light area at mesoposterior margin, 9th and 10th terga with variable-shaped mesoposterior light areas, preserved specimens may appear all brown, all yellow, or sometimes with thin posterior dark bands where anterior margins lie over ventral margins;
25 Abdominal terga with distinct, dark, anterior and posterior, transverse bands on segments 1–9, anterior bands sometimes thin, partially to completely hidden by overlapping segments margin, segment 10 usually with only anterior margin dark, with variable lateral dark banding;
25 Abdominal terga with distinct, dark, anterior and posterior, transverse bands on segments 2–9, anterior bands thick with mesoposterior margin modified slightly into variously rounded or emarginated median extensions, posterior bands thin;
segment one only with posterior transverse band thin, often faded in preserved material;

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

segment 10 with dark pigment variable, sometimes with a pair of median yellow transverse bands with some dark pigment near posterior margin;
25 Abdominal terga with distinct, dark, anterior, transverse bands on segments 1–10, first and 10th segments with bands completely faded after 7-months in 75% EtOH;
25 Abdominal terga usually with indistinct, thin, mesally interrupted, anterior and posterior dark transverse bands on segments 1–9, segment 1 anterior bands variably shaped, segment 10 with anterior band only and mesoposteriorly produced, these bands often faded in preserved material;

26 short, clear, clothing setae interspersed between stout spines;
26 long, dark, clothing setae interspersed between stout spines;
26 short, clear to golden clothing setae interspersed between stout spines;
26 short, clear, clothing setae interspersed between stout spines;
26 short, clear to golden, clothing setae interspersed between stout spines;
26 short, clear, clothing setae sparsely interspersed between stout spines;
26 long, dark, clothing setae sparsely interspersed between stout spines;
26 short, clear to golden, clothing setae interspersed between stout spines;

27 posterior margins with continuous row of spinules, those on 10th tergum usually a single, approximately linear row.
27 posterior margins with continuous row of spinules, those on 10th tergum usually a single, approximately linear row.
27 posterior margins with continuous row of spinules, those on 10th tergum sometimes in multiple rows along mesoposterior margin,
27 posterior margins with continuous row of spinules, those on 10th tergum single or multiple at mesoposterior margin.
27 posterior margins with continuous row of stout spines, those on 10th tergum usually multiple at mesoposterior margin.
27 posterior margins with continuous row of stout spines, those on 10th tergum usually multiple at mesoposterior margin.
27 posterior margins with continuous row of stout spines, those on 10th tergum usually in single, approximately linear row.
27 posterior margins with continuous row of spinules, those on 10th tergum sometimes in multiple rows along mesoposterior margin,

28 Posterior setal row of male 8th abdominal sternum sometimes interrupted mesally in mature and immature nymphs.
28 Posterior setal row of male 8th abdominal sternum usually interrupted mesally in mature nymphs.
28 Posterior setal row of male 8th abdominal sternum not interrupted mesally in mature nymphs, slightly interrupted in immature.
28 Posterior setal row of male 8th abdominal sternum interrupted mesally in at least mature nymphs.
28 Posterior setal row of male 8th abdominal sternum usually not interrupted mesally in mature nymphs.
28 Posterior setal row of male 8th abdominal sternum usually not mesally interrupted or with short interruption in mature nymphs.
28 Posterior setal row of male 8th abdominal sternum variable, from not mesally interrupted to short interruption in mature nymphs.
28 Posterior setal row of male 8th abdominal sternum usually not interrupted mesally in mature nymphs, slightly interrupted in immature.

29 Cercal segments golden brown;
29 Cercal segments yellow;
29 Cercal segments golden brown;
29 Cercal segments brown;
29 Cercal segments golden brown to dark brown;
29 Cercal segments golden brown to dark brown;
29 Cercal segments yellow;
29 Cercal segments golden;

30 apical whorl of short, stout setae, those located at mesoposterior apical margin becoming longer on distal segments.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl, except sometimes apical 9–10 segments with 1–5 slightly longer setae.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin becoming longer on distal segments.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.
30 apical whorl of short, stout setae, those located at mesoposterior apical margin similar in length to rest of whorl.

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Ova. —

1 General shape oval, triangular cross section (Fig. 23).
1 General shape oval, triangular cross section (Fig. 40).
1 General shape oval, triangular cross section (Fig. 61).
1 General shape oval, triangular cross section (Fig80).
1 General shape oval, triangular cross section (Fig. 99).
1 General shape oval, triangular cross section (Fig. 118).
1 General shape oval, triangular cross section (Fig. 137).
1 General shape oval, triangular cross section (Fig. 156).

2 Color light brown.
2 Color light brown.
2 Color light brown.
2 Color light brown.
2 Color light brown.
2 Color light brown.
2 Color yellow.
2 Color brown.

3 Length 229–249 µm, width 147 µm.
3 Length 385 µm, width 243 µm.
3 Length 380.5–482.9 µm, width 224.4–231.7 µm.
3 Length 414.6–448.8 µm, width 268.3–278.0 µm.
3 Length 395.1 µm, width 253.6 µm.
3 Length 409.7 µm, width 282.9 µm.
3 Length 414.6 µm, width 253.6 µm.
3 Length 448.9–497.6 µm, width 312.2–341.5 µm.

4 Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, without three large stabilizing carinulae at each anterior angle (Fig. 24).
4 Collar with slight apically flanged rim, stalked with slightly elevated and irregular carinae, and with 3 large stabilizing carinulae broadly connecting collar to each anterior angle (Fig. 41).
4 Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, with three large stabilizing carinulae at each anterior angle (Fig, 62).
4 Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, with three large stabilizing carinulae at each anterior angle (Fig. 81).
4 Collar with apically flanged rim, stalked with slightly elevated and irregular carinae, with 3 large stabilizing carinulae broadly connecting collar to each anterior angle (Fig. 100).
4 Collar with slight apically flanged rim, stalked with slightly elevated and irregular carinae, apical margin deeply incised between 3 large stabilizing carinulae that broadly connect to collar at each anterior angle (Fig. 119).
4 Collar with slight apically flanged rim, stalked with irregularly concentrated, small, globular processes, and with 3 large stabilizing carinulae broadly connecting to collar at each anterior angle (Fig. 138).
4 Collar with faint apically flanged rim; stalked with slightly elevated and irregular carinae, with three large stabilizing carinulae at each anterior angle (Fig. 157).

5 Chorionic surface granular (Fig. 24).
5 Chorionic surface smooth, with only very small, scattered globular structures (Fig. 42).
5 Chorionic surface with sparse, prominent, granular processes (Fig. 63).
5 Chorionic surface granular (Fig. 82).
5 Chorionic surface with dense, low globular processes (Fig. 101).
5 Chorionic surface granular (Fig. 120).
5 Chorionic surface mostly smooth, with granular processes concentrated and largest on angles (Fig. 139).
5 Chorionic surface granular (Fig. 158).

Isogenoides characters. Sequence corresponds with the 8 specific names in alphabetical order; e.g. *I. colubrinus* through *I. zionensis* as shown for male character 1.

6 Hexagonal follicle cell impressions absent.

7 Micropyle row subequatorial; orifices located on low slightly carinate, micropylar knobs (Fig. 25).
7 Micropyle row subequatorial; orifices located on low, smooth, rounded micropylar knobs (Fig. 42).
7 Micropyle row subequatorial; orifices located on low, smoothly rounded, micropylar knobs (Fig. 63).
7 Micropyle row subequatorial; orifices located within evenly raised, smoothly rounded, micropylar tubes (Fig. 82).
7 Micropyle row subequatorial; orifices located on low, smoothly rounded micropylar knobs (Fig. 101).
7 Micropyle row subequatorial; orifices located on long, irregular micropylar tubes (Fig. 120).
7 Micropyle row subequatorial; orifices located below short, smooth, elevated, cup-like sperm guides (Fig. 139).
7 Micropyle row subequatorial; orifices located within unevenly raised, slightly carinate, apical portions of micropylar tubes (Fig. 158). Occasionally orifices with upright, plate-like sperm guides.

LITERATURE CITED

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