A BIOSYSTEMATIC REVISION OF THE NEARCTIC SPECIES OF THE MAYFLY GENUS *ISONYCHIA* (EPHEMEROPTERA: OLIGONEURIIDAE)

by

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Dissertation submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Entomology

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June, 1982
Blacksburg, Virginia

"*Isonychia* is as remarkable a 'living fossil' as *Latimera*."

Edmunds (1975)

ACKNOWLEDGMENTS

I would like to thank my graduate committee for their invaluable advice and assistance in this study. Dr. J. R. Voshell, Jr. was extremely helpful in all aspects of this endeavor including financial assistance. I was fortunate to have the very helpful critical reviews of Drs. John L. Eaton, Michael Kosztarab, Richard L. Hoffman, and Brent D. Opell. I am indebted to them for their guidance and assistance.

Special thanks to fellow graduate students, Cliff Keil, Doug Howell, Joe Despins, Bob Zimmerman, John Deighan, Lorraine Los and Kevin Cannon for their technical assistance and counsel along the way. I would also like to thank Dr. James H. Kennedy, Ralph F. Kirchner, Dr. Charles R. Parker, Ms. Beth Umberger, Mr. Dan Campbell, and Dr. Frank L. Carle for their help in the field and laboratory.

I thank my wife, Penelope, whose understanding, advice, assistance and love made this task easier. This dissertation is dedicated to my mother, Professor Johanna Kondratieff, whose constant encouragement and assistance assured the completion of this study. I could have asked for nothing more.

I am deeply indebted to the following persons who allowed me to visit their respective institutions and examine large collections under their care: Drs. William L. Peters and R. Wills Flowers, Florida A & M University; Dr. George F. Edmunds, Jr., University of Utah; and Dr. Randall T. Schuh, American Museum of Natural History. Special thanks also to Harry M. Savage, Florida A & M University for rearing and associating for the first time *Isonychia sayi* and *I. arida*. We are indebted to the following persons for sending specimens: Lewis Berner, University of Florida; George F. Byers, University of Kansas; Philip J. Clausen, University of Minnesota; Ron S. Demaray, Lower Sackville, Nova Scotia; George F. Edmunds, Jr., University of Utah; Oliver S. Flint, Jr., Smithsonian Institution; R. Wills Flowers, Florida A & M University; Peter M. Grant, Florida A & M University; Brad C. Henry, Texas A & M University; David H. Kavanaugh, California Academy of Sciences; Paul K. Lago, University of Mississippi; Paul M. Liechti, State Biological Survey of Kansas; J. E. Martin, Canadian National Collection; Terry M. Mingo, University of Maine; Thomas E. Moore, University of Michigan; John C. Morse, Clemson University; Alfred F. Newton, Jr., Harvard University; L. L. Pechuman, Cornell University; William L. Peters, Florida A &

M University; Nancy Potthoff, Minnesota Department of Natural Resources; Arwin Provonsha, Purdue University; Selwyn S. Roback, Academy of Natural Sciences of Philadelphia; Harry M. Savage, Florida A & M University; Randall T. Schuh, American Museum of Natural History; Dan A. Soluk, University of Alberta; Bill P. Stark, Mississippi College, Margaret K. Thayer, Harvard University; John D. Unzicker, Illinois Natural History Survey; and Glenn B. Wiggins, Royal Ontario Museum.

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INTRODUCTION

The mayfly genus Isonychia is widely distributed in the Holarctic, Oriental and Neotropical regions. In the Nearctic realm, the genus is abundantly distributed, especially in eastern North America and southwestern United States. There are presently 25 species and 2 subspecies recognized in North America (Edmunds et al. 1976).

Isonychia nymphs and adults are important food for fish, especially trout (Leonard and Leonard 1962). Caucci and Nastasi (1975) list Isonychia bicolor (Walker) and I. sadleri Traver as important trout food in freestone mountain streams in eastern and central United States and producing exceptional fly-fishing. Schwiebert (1973) and McCafferty (1981) also illustrate and discuss several species of Isonychia that are significant as trout food and mention that these mayflies produce excellent "hatches."

Few comprehensive studies of the biology and ecology of either the immatures or adults of Isonychia are available. Presently, the most informative are: Clemens (1917), Cooke (1942), Berner (1959), Leonard and Leonard (1962), Edmunds et al.(976), Sweeney (1978), Wallace and O'Hop (1979), and Grant and Stewart (1980). The streamlined, negatively phototropic and strong swimming nymphs are unique in being one of the four mayfly genera in North America which are regarded as suspension or filter feeders (Edmunds et al. 1976). Filter feeders are an important component of the structure and function of aquatic ecosystems because they utilize the abundant small particles suspended in the water column and slow the export of energy from lotic ecosystems (Wallace et al. 1977, Merritt and Wallace 1981). Nymphs consume organic matter that has been strained from the water by the long setae on their forelegs. Wallace and O'Hop (1979) have provided a detailed description of the filtering feeding mechanisms of *Isonychia*.

The genus *Isonychia* originally was erected by Eaton (1871) to include his new species *manca* from Texas (type species) and *ignota* Walker, a Palearctic species. Later, he (1881) proposed the new name *Chirotonetes* to replace *Isonychia*, which he thought was preoccupied by *Isonychus* Mannerheim. McDunnough (1923) corrected Eaton's misinterpretation, discussing and using the correct name *Isonychia* for the genus known until then as *Chirotonetes* in North America. Previously Needham (1905) had reared *Chirotonetes albomanicatus* Needham and synonymized Eaton's (1881) Palearctic genus *Jolia* with *Chirotonetes* by proving that Eaton's figure of the type nymphs of "*Jolia roeselii*" was in fact the nymph of Chirotonetes, probably ignota, and that the presumed adult of J. roeselii was really a Palingenia (Palingeniidae). Recently Hubbard and Peters (1978) also synonymized the Pakistan genus Eatonia of Ali (1970) as another junior synonym of Isonychia.

Numerous workers described species from North America that were placed in the genus Isonychia: Say (1839), Walker (1853), Walsh (1862), Eaton (1871, 1885), McDunnough (1931), Needham (1932), Traver (1932, 1934), Berner (1948) and Burks (1953). Traver (1932, 1934) was the most prolific, describing 16 of the 25 currently known species. In 1931 McDunnough reviewed the genus in North America for the first time, describing two new species and one new subspecies and gave the first key to the species known from North America. He also suggested that male imagoes of the North American species could be readily divided into two distinct natural groups. Traver (1932) termed these groups the "arida" (= sayi Burks 1953) and the "albomanicata" (= bicolor of McDunnough 1931) groups. She further suggested that the "albomanicata" group could be subdivided into the sicca group using penes form. Traver (1935) redescribed all stages of species that were available and presented new keys, distributional data, and a bibliography of all known

North American species. She did not, however, accept McDunnough's (1931) contention that *I. albomanicata* was identical with *I. bicolor*. Kondratieff and Voshell (In press) formally divided *Isonychia* into two subgenera and four species groups based on a study of adult and nymphal characteristics. Several other authors have broadened the knowledge of the taxonomy, nomenclature and distribution of the genus in North America: Berner (1950), Burks (1953), Leonard and Leonard (1962), Allen and Cohen (1977) and Provonsha and McCafferty (1982)

Isonychia has had a very interesting familial classification history. The genus has been considered to have heptageniid (Spieth 1933) and baetid (Traver 1935) affinities. Also it has been included in the large inclusive family Baetidae (e.g. Traver 1935) and Siphlonuridae (e.g. Ulmer 1932-1933, Burks 1953, Edmunds 1973 and Edmunds et al. 1976). Burks (1953) finally erected the subfamily Isonychiinae in the Siphlonuridae to include the enigmatic *Isonychia*. Edmunds and Traver (1954) raised this subfamily to family rank without explanation, including *Isonychia* along with the genera *Coloburiscoides* Lestage (Australia), *Coloburiscus* Eaton (New Zealand), *Murphyella* Lestage (Chile, Argentina), and *Mirawara* Harker (Australia). However, Edmunds and Allen (1957) again included *Isonychia* in the Siphlonuridae as part of the subfamily Isonychiinae. Demoulin (1958) introduced another classification scheme and included Isonychia in the superfamily Oligoneurioidea in the family Isonychiidae and the subfamily Isonychiinae. Since then Isonychia has been variously included in Isonychiidae (mostly by European workers, e.g. Kimmins 1960, Demoulin 1969, Tshernova 1970) or the Siphlonuridae (mostly by North American workers, e.g. Edmunds 1973, Edmunds 1975, Edmunds et al. 1976). Recently McCafferty and Edmunds (1979) introduced another higher classification of the extant Ephemeroptera of the world and included Isonychia in the subfamily Isonychiinae of the family Oligoneuriidae. This classification was first introduced by Riek (1973). McCafferty and Edmunds made this placement based mostly on nymphal characteristics such as a double row of long filtering setae on the prothoracic femora and tibia, gills on the maxilla, tracheal system lacking a ventral cephalic branch, and the highly setaceous maxillae and labrum.

However, if adult characteristics such as wing venation, genitalia, and eggs are included, there is some doubt concerning the placement of this family. As Edmunds et al. (1976) and McCafferty and Edmunds (1979) mentioned, Isonychia has pregroup, group, and postgroup relationships with the Oligoneuriidae and Siphlonuridae. The intermediate position between these two families perhaps indicates that Isonychia should remain in its own family, Isonychiidae, or both the Oligoneuriidae and Isonychiidae be recombined again into the Siphlonuridae. Nevertheless, Isonychia is retained in the Oligoneuriidae in this treatment of the North American species because a thorough review of the higher classification is beyond the scope of this work.

Species taxonomy in Isonychia has been based on the adults. In general most of the original descriptions and redescriptions of the adults were too restrictive because of narrow "typological" color characteristics were used. Use of such narrow criteria does not allow for individual and population variability (i.e ecophenotypes). Modern workers (e.g. Bednarik and McCafferty 1979, Morihara and McCafferty 1979 and Pescador and Berner 1981) have shown that coloration and size of the stages of many mayflies vary with geographic locality and developmental rates

It is presently very difficult or impossible to identify most of species of Isonychia because some have been described more than once under different names and many of the original descriptions or redescriptions of the known stages have been too restrictive due to the use of color characteristics that are highly variable. Therefore the objectives of this study were to:

1. Provide comprehensive descriptions of species and identification keys for adults and nymphs of North American species.

2. Accurately define the species by incorporating biological information and determining the range of structural variation.

3. Provide information on the ecology of the different species.

4. Analyze the evolutionary history and dispersal of the Nearctic forms.

METHODS AND MATERIALS

Specimens were secured from most geographical regions of North America. Many specimens were provided by research institutions, including museums. Except for *Isonychia bicolor* (Walker) and *Isonychia intermedia* (Eaton), I was able to study type material of all species. The type material of *I. bicolor* (1 subimago female) was studied by Spieth (1940) and *I. intermedia* (1 male imago) was also studied by Spieth (1941). In these cases the specific validity and synomymies by Spieth were accepted. Both types are in the British Museum (Natural History). The male genitalia of all types of Traver's species are illustrated, since many of her original drawings were restricted to general characters.

Since the taxonomy of many of the North American species of *Isonychia* has been confused in part due to the poor condition of types and associated material and small sample size, extensive rearing and collecting were undertaken. Specimens were reared from North Carolina, Tennessee, Virginia, and West Virginia. All except three of the valid North American species were reared with all stages associated, many for the first time since their original description. All of Traver's type localities in North Carolina (6) were revisited.

Live nymphs were collected with a D-frame kick net or removed individually with a turkey baster. The turkey baster was especially useful for capturing mature nymphs that had migrated to quiet, shallow water for emergence. Nymphs were transported to the laboratory in styrofoam coolers containing several screen cages and a portable aerator. Nymphs were reared in a modified Living Stream (Frigid Units, Inc., Toledo, Ohio) in which water temperatures and photoperiods were adjusted to approximate field conditions. Individuals or group of nymphs were placed in cages made of fiberglass window screen. These cages were suspended in the water from a rack. Dry dog food was used as a food source for rearing nymphs to maturity. The dog food was ground into a fine powder using a Wiley Mill with a 20 mesh screen (mean particle size of 170.9 um x 106.6 um). This powder was thoroughly mixed with distilled water and small amounts were released in front of the screen cages with an eye dropper. Nymphs were observed cleaning their forelegs with their mouth parts after the suspended material passed. Nymphs grew rapidly at appropriate temperatures. Subimagoes were transferred to ventilated plastic jars for transformation. Nymphs and adults were preserved in Kahle's fluid and replaced with 80% ETOH and stored in shell vials.

Eggs of all valid species were examined by scanning electron microscopy according to the methods of Towns and Peters (1978). Photographs were taken with a AMR Model 900 Scanning Electron Microscope. Terminology of egg structure follows Koss and Edmunds (1974). Eggs were removed from associated imago females because eggs of late instar nymphs and subimagoes often were covered with suprachorionic adhesive layers (Koss and Edmunds 1974, Kopelke and Müller-Liebenau 1981).

Male and female genitalia and nymphal parts were mounted on slides by methods of Edmunds et al. (1976). All external structures were dissected in 80% ethanol and transferrred to xylene-free Canada balsam dissolved in cellosolve (ethylene glycol monoethyl ether). Nikon stereo zoom and compound microscopes were used to study whole and dissected specimens. Many of the illustrations were made with the aid of a microprojector. All specimens used for the species descriptions were preserved in alcohol.

The Munsell Book of Colors was used to judge colors of imago males from two different populations of I. bicolor (Sinking Creek and Little River, VA) to ascertain the variability of color hues over a single season. The Munsell system of color notation identifies three attributes: hue, value and chroma. The hue notation indicates its relation to red, yellow, green, blue, and purple; the value notation indicates its lightness, and the chroma notation indicates its strength (or departure from neutral). All color comparisons and color matching were identified using freshly preserved alcoholic material. At least five males per week throughout the season were viewed with a steromicroscope at about 90°with the light source at 45° . Identical illumination was employed for all observations.

In order to ascertain structural variability within populations, the life histories of three populations of two species were studied. A "two stage" D-frame kick net with coarse (0.9 x 0.8 mm mesh) and fine (100 um mesh) nets was used. This type of sampling device guaranteed the recovery of most early instars and helped prevent misinterpretations as outlined by Suter and Bishop (1980).

In the life history studies the following water quality measurements were taken: temperature (long-stem thermometer), pH (Beckman Electromate pH meter), alkalinity (Amer. Publ. Health Assoc. et al. 1975), dissolved oxygen (azide modification of the Winkler method, Amer. Publ. Health Assoc. et al. 1975) and conductivity (YSI Model 33).

All records and distributional ranges given for each species are based exclusively on specimens that I examined. Records given in the literature were omitted because of the uncertainty of many of the identifications. Specimens with obviously mislabeled or doubtful locality information were disregarded.

The following abbreviations are used for the sex and stage of specimens, the names of frequently reported collectors, and the institutions where material is housed.

M- male imago

F- female imago

N- nymph

BCK- B. C. Kondratieff

HTS- H. T. Spieth

JRT- J. R. Traver

LB- L. Berner

SSR- S. S. Roback

AMNH- American Museum of Natural History, New York

ANSP- Academy of Natural Sciences, Philadelphia

BH- Brad C. Henry, Jr., College Station, TX

CAS- California Academy of Sciences, San Francisco

CE- Clemson University, Clemson

CNC- Canadian National Collection, Ottawa

CU- Cornell University, Ithaca

DAS- D. A. Soluk, University of Alberta, Edmonton

FAMU- Florida A & M University, Tallahassee

FSCA- Florida State Collection of Arthropods, Gainesville

INHS- Illinois Natural History Survey, Urbana

MCZ- Museum of Comparative Zoology, Harvard University, Cambridge

NP- Nancy Potthoff, St. Paul Minnesota

PL- P.L. Liechti, State Biological Survey of Kansas, Lawrence

PU- Purdue University, West Lafayette

RD- R. S. Demaray, Nova Scotia

ROM- Royal Ontario Museum, Toronto

TM- T. M. Mingo, University of Maine, Orono

UK- University of Kansas, Snow Entomological Museum, Lawrence

UM- University of Michigan, Museum of Zoology, Ann Arbor

UMN- University of Minnesota, St. Paul

USNM- U.S. National Museum, Washington, D.C.

UU- University of Utah, Salt Lake City

VPI- Virginia Polytechnic Institute and State University, Blacksburg

Characters

The various Isonychia species show, with very few exceptions, little structural diversity, and are very similar in appearance.

Male Imago

Comparative coloration of leg segments, especially of the foretarsi, has been one of the common diagnostic characters used (e.g. the *bicolor* species group) for separating similar species. Color of the forelegs, reflects geographical, ecological and life cycle qualities and is therefore unreliable for species determination. Only in *I. arida* is foreleg coloration clearly diagnostic. Foreleg ratios of the femur to tibia, femur to tarsus, and various relative lengths of tarsal segments are not species specific. Traver (1935) previously used tibia/tarsal ratios for separating species of the "*sicca*" type. The ratio of the length of the second foretarsal segment to the first foretarsal segment is expresed as the foretarsal ratio.

Pigmentation of the forewing membranes is a useful character for separating several species of *Isonychia*. Both *I. tusculanensis* and *I. velma* have very characteristic pigmentation of the forewing membranes (Figs. 31-32), and *Isonychia edmundsi* imagoes usually possess dark pigmentation of the second and third bulla interspace (Fig. 33).

Use of various color shades (i.e "pale reddish", "darker red", "deep wine red", "deep red", "brighter red" and "dull rose red") have been the primary diagnostic characters utilized in this genus. These colors directly reflect geographical, ecological, and life history attributes, are generally useless for species determinations, and have resulted in unnecessary species splitting. However, most species or species groups tend to express a basic color pattern, which is usually the only reliable alternative for specific determinations. In the subgenus Prionoides, there are two types of color patterns. The most common (Figs. 23a-b) consists of an brownish-orange to brown abdominal ground color with a paler middorsal longitudinal stripe and dark submedian and lateral maculae. The second type is found only in I. sayi (Figs. 24a-b), consists of brown ground color with large yellowish anterolateral spots. In Isonychia s.s., the common abdominal color pattern is a reddish brown ground color with terga marked with blackish posterior marginal bands (Fig. 25). Many of the sicca group species have unique and diagnostic color patterns (Figs. 27-28).

Male genitalia, particularly the penes, are usually useful only for separating species groups of Isonychia s.s and delineating species in the subgenus Prionoides. Within Prionoides there is variability in the number of lateral and marginal teeth or serrations on the incurved medial flap within species. The usually acute anterolateral projections may or may not be toothed or have additional spines. Also for a single species the armature of the right lobe may differ slightly from that of the left lobe. In the bicolor species group of Isonychia s.s., the shape and size of the penes is correlated with individual size and geographical occurrence. Bednarik and McCafferty (1979) also documented this phenomenon in the genus Stenonema. Larger individuals and more northern populations tend to have relatively longer and narrower penial lobes, whereas smaller individuals or more southern populations have shorter and stouter penes. All penes should be examined only by using cavity slides or supported coverslips. Past problems in identification, especially with the subgenus Prionoides, have been due to distortion of the penes by standard slide mounting techniques.

Female Imago

Females generally exhibit few characters useful for distinguishing species. There are two basic shapes of the subanal plate. In the subgenus *Prionoides* the posterior margin is shallowly emarginate or often entire (Figs. 20-22). In *Isonychia* s.s. the posterior margin is moderately to deeply emarginate (Fig. 5).

Abdominal color patterns of females are only partially useful. Abdominal color intensity and pattern clarity depends on the absence (pattern indistinct) or presence (pattern distinct) of the whitish or yellowish eggs. Use of females void of eggs has contributed to some of the confusion in the taxonomy of the subgenus *Prionoides*.

Eggs

Eggs have been found to be useful for subgeneric and species-group characterization. Koss and Edmunds (1974) have described the eggs in detail. They did not, however have material of the subgenus *Prionoides* available for study.

Eggs are either biccnvex (subgenus Prionoides) (Figs. 72-95) or spherical (Isonychia s.s.) (Figs. 48-71) with no obvious poles. The knob-terminated coiled threads occur in several arrangements: (1) spaced in a uniform layer covering the entire egg (Fig. 50) or one hemisphere (Fig. 54); (2) localized in one specific region (Figs. 75-77); (3) scattered over surface (Fig. 60); and (4) spaced between ridges (Fig. 73). The terminal ends of the knob-terminated coiled treads are sometimes triangular (Figs. 59 and 80). The micropylar device is of the taganoform type (Fig. 88), the sperm guide is chorionic. These devices are present in the subgenus Prionoides on the side lacking the knob-terminated coiled threads (Figs. 78 and 86). Smith (1935) stated that eggs of I. rufa and I. manca were slightly flattened spheres. This is apparently an artifact of the eggs being closely appressed in the female body cavity.

Nymph

Nymphs are remarkably similar in structure and exhibt, not surprisingly, few useful diagnostic characters. Mouth parts (Fig. 34) are essentially invariable between all species. External head, thorax, and abdomen features are very similar among all species. Armature of tergal and sternal surfaces were examined closely by S.E.M. Terga and sterna both have very similar armature of variable position with scattered spines, setae and marginal serrations (Fig. 111). The armature of the caudal filaments is also very similar among all species (Fig. 112). The armature of the legs is occasionally characteristic in some species groups. The number and position of the stout foretibial spines is characteristic for some species. Generally, species of Isonychia s.s have fewer leg spines than those of Prionoides. The length of the tibial spur relative to the foretarsi, a character used by Traver (1935) for species characterizations is highly variable and, as Berner (1950) already noted, useless as a diagnostic character.

The structure of the different types of gills was found to be a very useful diagnostic character. There are two forms of forecoxal gills. In all species of the subgenus Prionoides (except I. sayi), the forecoxal gill is a stout single filament (Fig. 103), whereas in

<u>Isonychia</u> s.s. the gill is the more characteristic tuft of multibranched filaments (Figs. 104-105).

The marginal armature of the abdominal gill lamella is a consistent and significant diagnostic character for separating the two subgenera. Mature nymphs of the subgenus <u>Prionoides</u> have gills 1-7 (always 6-7) without stout spines on the apical margins (Figs. 47 and 110); those of <u>Isonychia</u> s.s have gills 1-7 (always 6-7) with stout spines on the apical margin (Figs. 46 and 109). The surface armature of the gill lamella is apparently useful in separating the <u>sicca</u> species group of <u>Isonychia</u> s.s. from the <u>bicolor</u> and <u>arida</u> species groups. Generally the <u>sicca</u> species have the sclerotized distal edge of the anterior margins with three or more indistinct rows of spines (Fig. 106) and the median sclerotized ridge with a distinct row of spines (Fig. 107), whereas the <u>bicolor</u> and <u>arida</u> group species usually possess two or less rows of spines (Fig. 108) and no distinct row of spines on the median sclerotized ridge. These characters should be used with caution, and numerous nymphs of a single population should be examined.

Potential taxonomic value of the microtrichia of the double row of long filtering setae of the forelegs was first mentioned by Wallace and O'Hop (1979). However, specimens examined in this study indicated structural variation. Most species of the subgenus Prionoides have an arrangement similar to Figs. 7-8 presented by Wallace and O'Hop and generally Isonychia s.s. have an ultrastructure similar to their Figs. 3-4.

In several cases the only alternative to use is color or color patterns for separating similar species. In these instances a series of nymphs should be studied. In I. bicolor, color and color patterns are highly variable.

It is interesting to note that body and gill surfaces of nymphs often had the diatom Cocconeis placentula var. euglypta (Ehrenberg) Cleve. attached (Fig. 113). This diatom was common on nymphs from most geographic regions, especially of the sicca and bicolor species groups.

Immature nymphs of the subgenus Prionoides are often quite striking. They often exhibit a beautiful mottled appearance of light brown with middorsal brownish streaks and whitish submedian streaks and lateral spots.

SYSTEMATIC ACCOUNTS AND KEYS

Genus *Isonychia* Eaton

Isonychia Eaton, 1871: 33, 134. Type species: *Isonychia manca* Eaton, by original designation; McDunnough, 1923: 46; McDunnough, 1931: 157; Traver, 1932: 200; Spieth, 1933: 329; Traver, 1935: 477; Berner, 1950: 106; Berner, 1959: 36; Burks, 1953: 108; Koss and Edmunds, 1974: 303; Landa, 1969: 295; Edmunds et al., 1976: 144; Hubbard and Peters, 1978: 31; Kondratieff and Voshell, (In press).

Chirotonetes Eaton, 1881: 21. Type species: *Isonychia manca* Eaton, by direct substitution; Needham, 1905: 28; Ulmer, 1920: 134.

Jolia Eaton, 1881: 192. Type species: *Palingenia roeselii* Joly, by original designation.

Eatonia Ali, 1970: 121. Type species: *Eatonia khyberensis* Ali, by monotypy; Hubbard and Peters, 1978: 31.

Male Imago:

Body: length 8-18 mm, forewings 8-17 mm.

Head: Compound eyes meet on meson of head, usually obliquely transverse light or darker bands separating upper from lower portion; Remnants of gill tufts (often purplish) at base of vestigial maxillae.

Thorax: Prothoracic leg various shades of brown, meso- and metathoracic leg whitish or yellowish. Forelegs usually subequal to body; foretibia usually subequal to foretarsus; foretarsal ratio: .60-1.15; base of forecoxae with remnants of gill tufts or of single gill filament. Mesosternum and metasternum with spinous median processes at anterior margins, mesosternum also with spinous median process submedially. Forewings with typical siphlonurid venation, costal angulation of hind wings obtuse (Figs. 29-30).

Abdomen: 10 segments; subgenital plate posteriorly broadly or slightly emarginate (Fig. 15e) or with a deep posteromedian emargination (Fig. 2-3 and 9) forceps 4-segmented, sometimes appearing 5-segmented; penes either dorsally with incurved medial flaps with sclerotized lateral and marginal serrations and spines (Figs. 14-19b), or lobes dorsally with a slightly sclerotized spinous flap on medial edge (Figs. 1-4) or at most with only a slightly sclerotized medial margin

(Figs. 8-13); two caudal filaments present, terminal filament vestigial.

Female Imago:

Body: length 9-19 mm, forewings 9-18 mm.
Similar to male in appearance and structure. Compound eyes small, widely separated on meson. Subanal plate with posterior margin with no or slight (Figs. 20-22) to deep emargination (Fig. 5).

Mature Nymph:

Body length 8-22 mm.
Head: Hypognathous; median frontal carina below median ocellus, distally acute; antennae 2-3 times width of head, inserted below eyes. Mouthparts heavily setose (Figs. 34 and 102), anterior margin of labrum with a broad shallow emargination (Fig. 34) strong dorsal setae present, additional setae in broad V-arrangement ventrally, maxillae with 2- segmented palps, apical segment setose, galea-lacina setose with 2 stout apical spines (Fig. 34); maxillary gills multibranched; mandibles with inner and outer incisors with 3 large apical teeth (Fig. 34); labium with paraglossae and glossae separated and setose, apical segment of palp

setose (Fig. 34); hypopharynx with linqua broadly rounded, superlinqua laterally developed (Fig. 34).
Thorax: Legs with many stout spines; foretibiae with long apical spur, inner surface of forefemora and foretibiae with double row of long setae(Fig. 35); procoxal gills either as tufts of multibranched filaments (Fig. 104-105) or a single robust filament (Fig. 103) tarsal claws denticulate.
Abdomen: Pair of gills on segments 1-7, dorsal lamella similar in shape, broadly rounded to subtruncate at apices, fibrilliform portion conspicuous, multibranched; posterolateral spines on segments 4-8; cerci slightly longer than terminal filament with long inner marginal setae, terminal filament with long inner and outer marginal setae.

Keys

Adults as a rule are only reliably distinguishable to the specific level using male imagoes. A key to the females is only presented for the subgenus Prionoides. All characters used in the keys are subject to some variation. Series of males should be carefully examined, especially in the subgenus Prionoides for penial variability.

The nymphal key is based on fully-mature specimens with swollen or dark wing pads and is intended for use only with mature nymphs. Nymphs of Isonychia are notoriously similar and must be carefully examined in series. Therefore, the following keys to the nymphs are not always reliable, but are more useful than previously available.

Key to the Nearctic Subgenera and Species Groups of *Isonychia*

Male Imagoes

1. Subgenital plate broadly concave or with only slight posteromedian emargination (Fig. 15e); penes dorsally with acute sclerotized lateral and marginal serrations and large spines on incurved flap (Figs. 14-19b) - - - - - - - - - - - - - - - - - - - subgenus *Prionoides*

   Subgenital plate with deep posteromedian emargination (Figs. 2 and 9); penes dorsally without incurved flap bearing sclerotized teeth or serrations (Figs. 1-3 and 8-13) - - - - - - - - - - - subgenus *Isonychia* s.s. - - - - - - - - - - - - - 2

2. Penes boletoid (Fig. 13) - - - - - - - - - - *diversa* group, *I. diversa*

   Penes not mushroom-like (Figs. 1-3 and 8-12) - - - - - - - - - - - - 3

3. Foretibia white, dark brown at base and at apex (Fig. 7); penes as Fig. 6 - *arida* group, *I. arida*

   Foretibia entirely brownish, sometimes dark brown at base and apex, penes as Figs. 1-3 - 4

4. Penes with prominent lightly scolerotized dorsal flap at medial edge; ventral lobes with posterior margin usually undulate (Figs. 1-3) - *I. bicolor* group

   Penes without prominent lightly sclerotized dorsal flap at medial edge; at most with only a slightly sclerotized medial margin; ventral lobes very broadly rounded or subtruncate posteriorly (Figs. 8-12) - *I. sicca* group

Female Imagoes

1. Subanal plate with no or only slight broad posteromedian emargination (Figs. 20-22) - - - - - - - - - - - subgenus Prionoides

   Subanal plate with a moderate to deep posteromedian emargination (Fig. 5) - subgenus Isonychia s.s.

Mature Nymphs

1. Abdominal gill lamella without apical stout marginal spines (Figs. 47 and 110); forecoxal gills a single robust filament (Fig. 103) (except I. sayi) - - - - - - - - - - - - - - - - - - subgenus Prionoides

   Abdominal gill lamella with apical stout marginal spines (Figs. 46 and 109); forecoxal gills in tufts of multibranched filaments (Figs. 104-105) - - - - - - - - - - - - - - - subgenus Isonychia s.s.

Key to Mature Nymphs

of the Subgenus Isonychia

1. Sclerotized distal edge of anterior margin of abdominal gill lamella 6-8 usually with 3 or more indistinct rows of stout spines (Fig. 106) and median sclerotized ridge usually with a row of spines along entire length (Fig. 107); species of southwestern, central and southeastern North America (Maps 6-10) - sicca group - - - - - - - - - - - - - - - - - 6

   Sclerotized distal edge of anterior margin of abdominal gill lamella 6-8 usually with 2 or less indistinct rows of stout spines (Fig. 108) and median sclerotized ridge usually only with scattered stout spines; species of eastern and central North America (Maps 1-3 and 5) - - - - - - - bicolor and arida groups - - - - - - - - - - - - - 2

2. Foretibia bicolored (dark brown at base and apex, whitish medially) as visible through cuticle (Fig. 7) - - - - - - - - - - - arida (Say)

   Foretibia entirely brown as visible through cuticle - - - - - - - 3

3. Distribution California and Oregon (Map 4); length of mature nymph 17-22 mm; general body color rather uniform dark yellowish brown - velma Needham

   Distribution eastern and central North America (Maps 1-3); length of mature nymphs 7-17 mm; general body shades of brown with paler markings - 4

4. Wide pale middorsal abdominal stripe distinctly bordered by dark brown (Fig. 43); limited distribution (Map 3) - tusculanensis Berner

Middorsal abdominal stripe variable, if present usually not distinctly bordered by dark brown; widespread distribution (Maps 1 and 2) - 5

5. Ventral apical cleft of metathoracic femur with usually 6 or more stout marginal spines (at least on one leg) (Fig. 36); distribution eastern and central North America (Map 1) - - *bicolor* (Walker)

   Ventral apical cleft of metathoracic femur with usually 5 or less stout marginal spines (Fig. 37); distribution central North America (Map 2) - - - - - - - - - - - - - - - - - - - *rufa* McDunnough

6. Dorsal apical leading edge of prothoracic femur with numerous stout spines as Fig. 39; length of mature nymph 16-21 mm - *intermedia* (Eaton)

   Dorsal apical leading edge of prothoracic femur with fewer stout spines as Fig. 40; length of mature nymph 14-17 mm - - - - - - - - - - - - - - - - - - *campestris* McDunnough, *edmundsi* n. sp., *sicca* (Walsh)

Key to Male Imagoes

of the Bicolor Group

1. Apical half to third of forewing uniformly shaded with brown (Fig. 31) - tusculanensis Berner

   Apical half to third of forewing hyaline, occasionally very faintly tinged with reddish-brown - - - - - - - - - - - - - - - - - 2

2. Venation reddish-brown with costal and subcostal spaces of forewing tinged with red or reddish-brown, crossveins heavily margined with red or reddish-brown (Fig. 32); distribution limited to California and Oregon (Map 4) - velma Needham

   Venation whitish to brown with costal and subcostal spaces of forewing not tinged with red or reddish-brown, only stigmatic region tinged with whitish opaque or brown; distribution eastern and central North America (Maps 1 and 2) - - - - - - - - - 3

3. Penes dorsally with a prominent basal dome-like swelling forming lateral and apical ridges (Figs. 2 and 100-101); venation of forewings whitish to light yellowish; stigmatic crossveins of forewings usually anastomosed; abdominal terga usually bright reddish to reddish-orange brown; central North America (Map 2) - rufa McDunnough

   Penes dorsally without a prominent basal dome-like swelling, at most only with lateral ridges (Figs. 1-3 and 96-97); venation of forewings whitish to dark brown; stigmatic region of forewings usually with no or only a few anastomosed crossveins; abdominal terga usually dark reddish-brown to dark red, occasionally orangish red; eastern and central North America (Map 1) - _bicolor_ (Walker)

Subgenus Isonychia Eaton, sensu stricto

Type species: Isonychia manca Eaton, original designation.

Male Imago:

Body: length 8-16 mm, forewings 9-15 mm.
Abdomen: Generally light brown to dark reddish-brown with posterior margins of terga purplish-black; often with a faint middorsal stripe and submedian streaks or spots; sometimes with darker median and lateral streaks or one species with large anterolateral yellowish spots.
Genitalia: Subgenital plate with deep posteromedian emargination (Figs. 2-3 and 9); forceps 4-segmented sometimes appearing 5-segmented; penes without incurved and serrated flap; anterolateral angles rounded.

Female Imago:

Body: length 9-16 mm, forewings 9-15 mm.
Subanal plate: With moderate or deep posteromedian emargination (Fig. 5).

Egg: Spherical with knob-terminated coiled threads densely covering egg or densely covering one hemisphere, scattered in the other or scattered over entire chorion or covering one hemisphere, absent on the other.

Nymph: Abdominal gill lamella with stout spines on apical margin (Fig. 46); procoxal gills in tufts of multibranched filaments (Fig. 104).

Diagnosis:

Male and female imagoes of Isonychia s.s. are easily distinguished from the following subgenus, Prionoides, by any of the following characters: (1) subgenital plate with a deep posteromedian emargination, (2) penes dorsally lacking a incurved serrated medial flap, (3) subanal plate with a moderate to deep posteromedian emargination, and (4) eggs spherical.

Mature nymphs of Isonychia s.s. are distinguished from the subgenus Prionoides by possessing stout spines on the apical margins of all abdominal gill lamella and forecoxal gills are always in the form of a tuft of multibranched filaments.

Bicolor Group

Male Imago:

Genitalia: Penes with anterior margin of ventral lobes usually undulate; apices of dorsal lobes with a prominent slightly sclerotized flap on the medial edge (Figs. 1-3).

Isonychia (Isonychia) bicolor

(Walker)

Figs. 1, 25, 29, 36, 41, 42, 48-52, 96-99, 104, 105, 108, 109

Palingenia bicolor Walker, 1853: 552. Type locality: St. Martin's Falls, Albany River, Hudson's Bay, Ontario, Canada, F subimago. Type deposition: British Museum; Hagen, 1861: 43.

Siphlurus bicolor, Eaton, 1871: 128; Eaton, 1885: 221.

Chirotonetes albomanicatus Needham, 1905: 31. Type locality: Ithaca, New York, M, F, nymph. Type deposition: (M) CU.

Isonychia albomanicata, Traver, 1932: 203; Traver, 1935: 483.

Isonychia bicolor, McDunnough, 1931: 161; Traver, 1932: 201; Spieth, 1940: 326; Traver, 1935: 486; Burks, 1953: 113; Leonard and Leonard, 1962: 80.

Isonychia pacoleta Traver, 1932: 218. Type locality: Pacolet River, near Tryon, North Carolina, M, F, and nymph. Type deposition: (M) CU; Traver, 1935: 494. New Synonym

Isonychia christina Traver, 1934: 240. Type locality: Ithaca, New York, M, F. Type deposition: (M) CU; Traver, 1935: 487. New Synonymy

Isonychia circe Traver, 1934: 242. Type locality: Chattahoochee River, Atlanta, Georgia, M, F. Type deposition: (M) CU; Traver, 1935: 488; Traver, 1937: 81. New Synonymy

Isonychia fattigi Traver, 1934: 245. Type locality: Swamp Creek, Dalton, Georgia, M, F. Type deposition: (M) CU; Traver, 1935: 489; Traver, 1937: 81. New Synonymy

Isonychia harperi Traver, 1934: 246. Type locality: St. Regis River, Fort Jackson, New York, M, F. Type deposition: (M) CU; Traver, 1935: 491; Leonard and Leonard, 1962: 82. New Synonymy

Isonychia matilda Traver, 1934: 248. Type locality: Wild Flower Preserve, Slaterville, New York, M, F and nymph. Type deposition: (M) CU; Traver, 1935: 492. New Synonymy

Isonychia sadleri Traver, 1934: 251. Type locality: Fish Hatchery on Cascadilla Creek, Ithaca, New York, M, F. Type deposition: (M) CU; Traver, 1935: 496; Traver, 1937: 59; Leonard and Leonard, 1962: 80. New Synonymy

Male Imago:

Body: length 9-16 mm, forewing 10-15 mm.

Head: Eyes grayish red to grayish purple with dorsal portion separated by lighter and darker transverse bands; ocelli grayish; ocellar elevations dark brown to black; a brownish spot between compound eyes and scape. Antennae yellowish to brownish-red, usually lighter distally. Margin of transverse shelf reddish or purplish red.

Thorax: Mesonotum yellowish-brown to dark reddish; metanotum light brown to blacklish-brown. Pleura yellowish to brownish with membranes often tinged with purple or red. Prothoracic leg reddish-brown to dark brown, femur often lighter brown or yellowish basally, tarsi ranging from whitish or grayish to brown, joints often darker, claws grayish to brown; meso- and metathoracic legs whitish or yellowish, tarsi and claws often tinged with brown or purple. Wings hyaline with venation whitish to brown, stigmatic region of forewing usually stained white or brown, stigmatic crossveins with or without anastomosing (Fig. 29); in very dark forms apical portion of forewings appearing lightly tinted with brown.

Abdomen: Terga orangish to reddish-brown to dark reddish-brown; terga 1-9 with purplish-black to blackish bands on posterior margins (Fig. 25); terga 2-6(7) occasionally with narrow translucent posterior bands; terga 7-10 often lighter in color (chalky white to light red); terga 2-9 usually with pair of submedian light or dark oblique streaks and/or often with lighter middorsal stripe. Pleural fold often margined with dark brown to black or gray; terga 2-8 with black dash below pleural fold. Sterna orangish to dark brown; sterna 1-9 usually with light purplish-black bands on posterior margins; sterna 2-9 usually with a midventral pair of pale streaks and spots. Caudal filaments whitish to yellowish to brown, if whitish to yellowish, basal portion shaded with brown and several basal articulations marked with reddish or brown. Forceps yellowish to reddish-brown. Genitalia variable (Figs. 1a-h).

Female Imago:

Body: length 11-17 mm, forewings 10-16 mm.

Head: Yellowish to brown; ocelli whitish or grayish; ocellar elevations blackish; dorsally often with a pair of dark stripes. Posterior angles of occiput dark brown to black; a dark brownish or blackish bar to a spot between compound eye and scape. Antennae yellowish to grayish.

Thorax: Mesonotum yellowish to reddish-brown; metanotum light brown to dark brown. Pleura yellowish to brownish, membranes tinted with red or purple. Prothoracic leg reddish-brown to brown, femur often lighter brown basally, tarsi whitish or brownish; meso- and metathoracic legs whitish to yellowish, tarsi and claws tinged with brown or purple. Wings hyaline with venation whitish to brownish; stigmatic region of forewing stained whitish to brownish, stigmatic crossveins with or without anatomosing.

Abdomen: Terga orangish to reddish-brown to dark brown; terga 1-9 with purplish black to blackish bands on posterior margins; terga 2-6(7) occasionally with narrow translucent bands posterior of blackish bands; terga 2-9 often with a pair of middorsal light or dark streaks and/or lighter middorsal stripe. Pleural fold usually margined with brown, black or gray. A black dash or spot below pleural fold (terga 2-8). Sterna 2-9 usually with a midventral pair of light streaks and spots. Caudal filaments colored as male. Subanal plate moderately to deeply emarginate (Fig. 5).

Egg: Typical of subgenus, but variable in density of knob-terminated coiled threads packed on one hemisphere, scattered on surface or densely covering entire egg (Figs. 48-53).

Nymph:

Body: length 6-18 mm.

Head: Yellow brown to dark brown usually with whitish or light yellow coronal stripe, stripe often with edges mottled with brown dorsally. Antennae varying from whitish to light brown; scape and pedicel brownish or whitish, basal flagellar segments often tinged with brown.

Thorax: Nota yellowish-brown to brown usually with a whitish or yellowish middorsal stripe, stripe often faint or absent; pronotum with 2 pairs of submedian whitish crescentric spots and sometimes a middorsal pair of whitish dots; whitish or yellowish (often faint) spots and streaks anterior and lateral of mesothoracic wing pads; mesothorax often with a pair of whitish median and submedian spots. Legs brown with yellowish marks; forefemora brown either with distinct or faint basal, median and apical spots or transverse bands;, tibia whitish to yellowish-brown with median brown transverse band, entire tibia sometimes mottled with brown, tarsi usually yellowish with a wide transverse band, occasionally entire tarsi brown; tarsal claws with 5-11 marginal denticles. Procoxal gills in tufts of multibranched purplish filaments. Abdomen: 4 general abdominal color patterns: (1) terga dark golden yellow with anterior and posterior transverse bands dark brown (Fig. 41); terga 1-4(5) with yellow middorsal stripe, often faint, center of stripe often with brownish streak or blotch; terga 5-9 with stripe margined with diffuse brownish submedian oblique streaks or blotches. Sterna dark brown with anterolateral spots or streaks, (2) terga dark reddish-brown; terga 1-9 with a wide yellowish middorsal stripe (Fig. 42); mediolateral margins of terga 1-9 with yellowish spot; posterolateral angles of terga 1-9 yellowish. Sterna reddish brown with faint medial light marks, (3) terga light brown; terga 1-4(5) with distinct middorsal stripe; terga 5-9 with either diffuse and faint or no middorsal stripe; mediolateral edge of terga 1-9 yellowish. Sterna light brown; sterna 2-8(9) with pair of light yellowish oblique streaks, and (4) terga light to dark brown with no middorsal stripe. Gill lamella light gray to purplish often with 1 or 2 diffuse purplish or brownish spots in distal margin. Median sclerotized ridge brown. Fibrillar portion whitish to purplish. Caudal filaments yellowish to dark brown, each filament usually with a brown or blackish cross band near middle and near tip, between these bands, filaments usually whitish.

Diagnosis:

Isonychia bicolor is a very variable species. Male imagoes are distinguished from all other species of the bicolor group by the following combination of characters: (1) wings hyaline, venation whitish to brown, (2) dorsally, penes without basal dome-like swelling not forming distinct apicolateral ridges, (3) abdominal color usually dark reddish-brown to dark red, sometimes orangish, and (4) forewings often without stigmatic crossveins anastomosed.

Within the bicolor group, imago males of I. bicolor may be confused with the closely related I. rufa. However, I. bicolor may be distinguished from the sympatric I. rufa by the characteristics listed above. Also all collections examined where _I. bicolor_ and _I. rufa_ overlapped in distribution, the dark reddish-brown abdominal color of _I. bicolor_ usually distinguishes it from the brighter reddish color of _I. rufa_. The character used by Burks (1953) for separating these two species, "forewing with stigmatic crossveins relatively numerous and anastomosed," versus "forewings with stigmatic crossveins relatively few and not anastomosed" was often not reliable. Dark and higher elevational forms of _I. bicolor_ usually have numerous anastomosed stigmatic crossveins. Also generally all populations of _I. bicolor_ examined contained individuals with some anastomosing of the stigmatic crossveins. Conversely, populations of _I. rufa_ examined, particularly from its more southern ranges, contained individuals with no or only a few stigmatic crossveins anatomosed.

The nymph of _I. bicolor_ is similar to _I. rufa_ and _I. tusculanensis_ (See remarks concerning identification under these species).

Biology:

Almost all of the life history and ecological information reported for the genus *Isonychia* in North America concerns *I. bicolor*. The most comprehensive studies are by Clemens (1917), Sweeney (1978) and an unpublished study by Smith (1978). Several other authors provide brief biological information on *I. bicolor*: Needham (1905), Morgan (1911, 1913), Ide (1935b), Cooke (1942), Leonard and Leonard (1962), and Harper and Magnin (1971). Ide (1935b) described and figured the egg and instars I and II of *I. bicolor*. Sherberger et al. (1977) studied the drift of aquatic insects through thermal plumes. They indicated that *Isonychia* (*I. bicolor*) nymphs were tolerant to thermal shock, and that these shocks apparently did not affect rheotaxis, phototaxis, substrate orientation, or susceptibility to predation.

Smith (1978) and Sweeney (1978) found *I. bicolor* to be bivoltine with a spring and summer generation. Sweeney's study showed that female subimago body size and fecundity for the overwintering spring emerging generation was about double that of the smaller summer emerging generation. His study indicated that temperature affected both nymphal tissue growth and the rate of adult tissue maturation, and therefore was a key factor in determining the distribution, life history, and fecundity of _I. bicolor_.

The life history and ecology of _I. bicolor_ was analyzed in two different streams in Virginia where it seemed that _I. bicolor_, _I. christina_, _I. matilda_, and _I. sadleri_ occurred sympatrically over a single season.

Samples were collected in all habitats (riffles to backwaters) at each of the following study sites with the "two stage kicknet." Samples were collected monthly from November to March and about every two week for the remainder of the year. Additional nymphs were collected for rearing and structural analysis. To assist in elucidating emergence and flight periods, a white light or black-light placed on a white sheet of cloth were used to collect subimagoes and adults throughout the warm months. Other data such as timing, place of emergence, and flight patterns were recorded from direct field observations.

Sinking Creek is a tributary of the New River Basin in the Ridge and Valley Province of Virginia. The stream originates from a series of springs. The substrata at the sampling site (Newport Park, Newport,

Table 1. Average water quality parameters, Sinking Creek, Giles Co., Va. from January 1981 to January 1982 (ranges in parenthesis).

Dissolved oxygen (ppm)	10.5 (8.6 - 13.0)
Dissolved oxygen saturation (%)	109 (96 - 119)
Hydrogen ion concentration (pH)	8.0 (6.80 - 8.70)
Total alkalinity (ppm $CaCO_3$)	97 (83 - 121)
Specific conductance (μmhos)	154 (90 - 328)

Table 2. Average water quality parameters, Little River, Montgomery Co., Va. from January 1981 - January 1982 (ranges in parenthesis).

Dissolved oxygen (ppm)	8.8 (7.1 - 12)
Dissolved oxygen saturation (%)	99 (82 - 116)
Hydrogen ion concentration (pH)	6.6 (6.4 - 7.2)
Total alkalinity (ppm $CaCO_3$)	21 (15 - 24)
Specific conductance (μmhos)	119 (114 - 130)

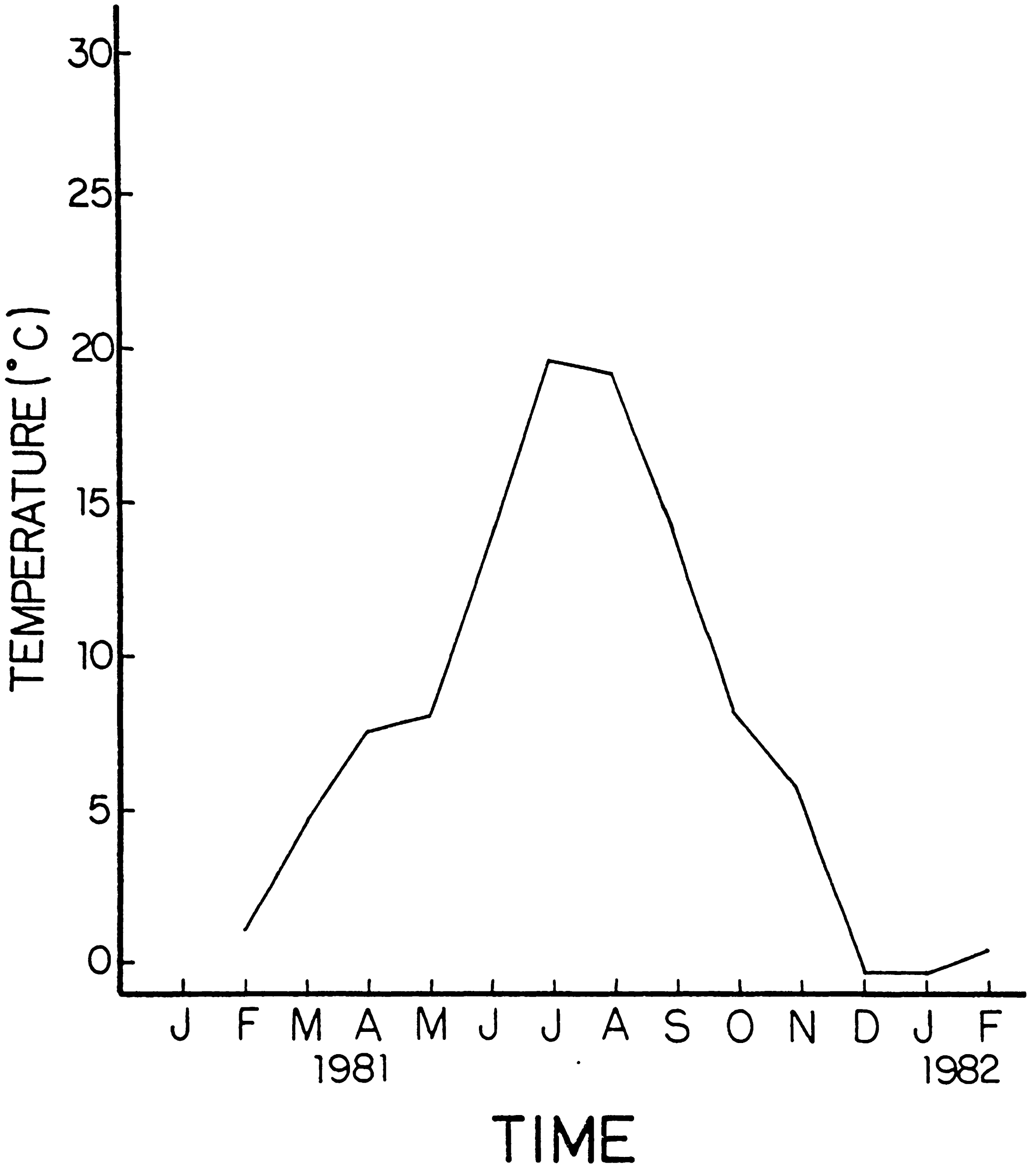


Fig. 1a. Water temperatures in Sinking Creek, Va.

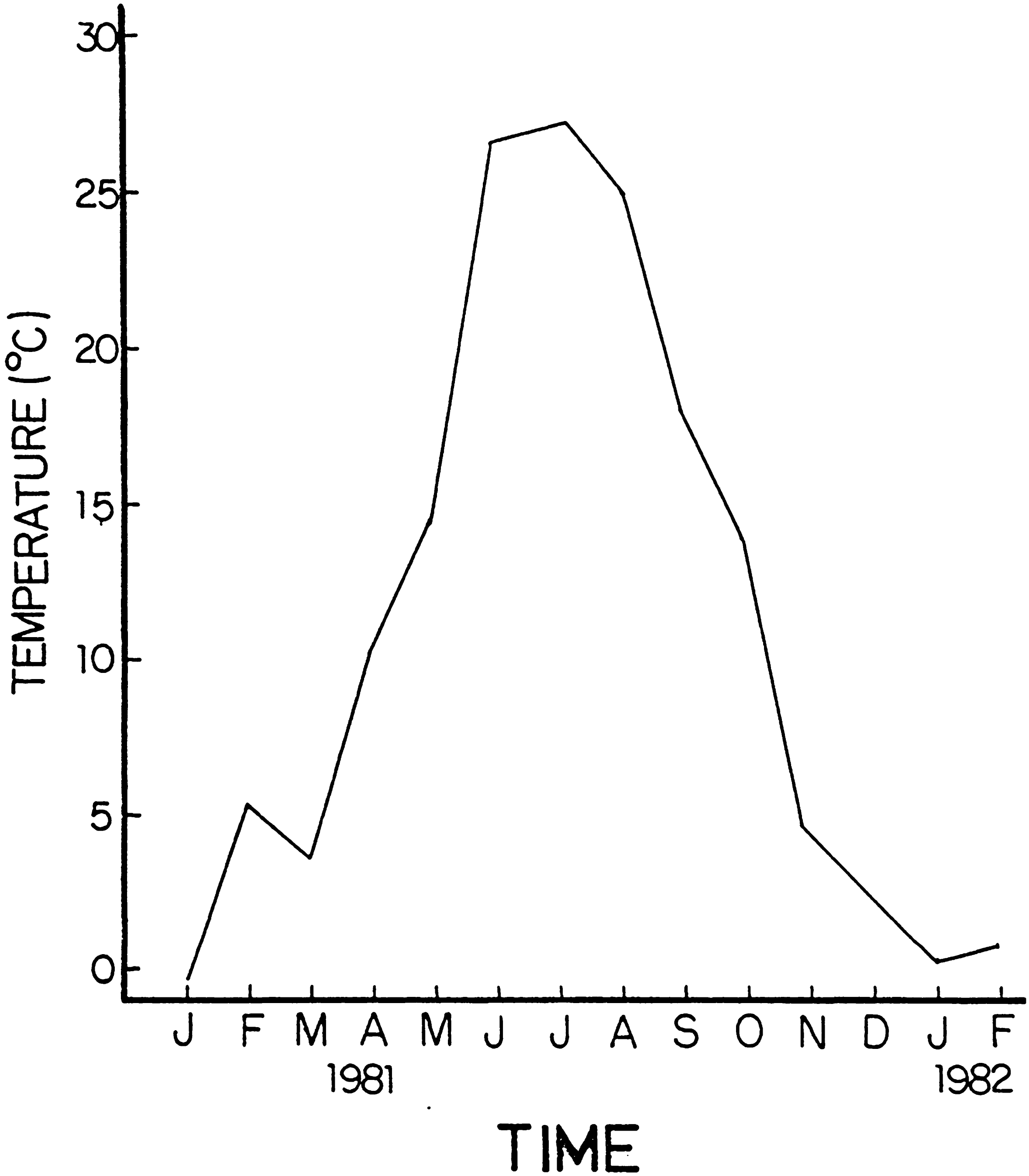


Fig. 2a. Water temperatures in Little River, Va.

Newport, VA) was exposed bed rock, with overlying coarse pebble (32-64 mm), and some cobble (24-256 mm). At the sampling site the stream was 4th order and had a good canopy of Eastern Hemlock (Tsuga canadensis (L.) Carr.), Flowering Dogwood, (Cornus florida L.), and Rosebay Rhododendron. (Rhododendron maximum L.). Water temperatures at this site ranged from -1°C to 24 °C (Fig. 1a). Other physical-chemical parameters are listed in Table 1.

The Little River, a tributary of the New River (New River Basin), lies within the Ridge and Valley Province in Montgomery County, Virginia. A sampling site was established at County Route 787. At this point the river was a 4th order stream. The substrata consisted primarily of pebble (16-64 mm) with some cobble (64-256 mm). Thick mats of Podostemum ceratophyllum Michaux (river weed) occurred on the substrate in the faster riffles. Water temperatures ranged from -1°C (January) to 28°C (June) (Fig. 2a). ther water quality parameters are listed in Table 2.

The subimagoes of I. bicolor emerged in late morning to late afternoon at both sites, however, the method of emergence was different at each site. At

Sinking Creek, the nymphs crawled 12-15 cm above the water surface onto rocks and other protruding objects before the subimagoes emerged. Usually the spring-emerging nymphs crawled further away from the edge of water then the summer and fall emerging-nymphs. At the Little River site nymphs would either just cling to projecting rocks or debris of shallow stream side margins or large projecting rocks in riffle areas not leaving the water. After emerging, subimagoes at both sites flew high into nearby vegetation. The average duration of the subimago stage was 20-36 hours at both streams.

There was seasonal size variation among adults only from Sinking Creek. Mean total body length was greatest in May (M 15-16 mm, F 16-18 mm) and least in August - October (M 10-11 mm, F 11-13 mm). At the Little River site mean total body length averaged ca. 10-11 mm for males and 11-13 mm for females throughout the season. There was also marked variation in fecundity throughout the season at Sinking Creek. Spring-emerging adults averaged 3000 eggs/female (n=5), while the summer and fall adults averaged only 940 eggs/female (n=5). At the Little River site, there was little variation (878-1040) throughout the season, with an average of 958 eggs/female (n=10).

Large nuptial flights were observed at both streams. At Sinking Creek nuptial flights lasted from early evening to after dark, with large flights of males (30-75 individuals) rhythmically rising and descending 3-5 m over riffles, occasionally almost touching the waters surface. Females would fly into these swarms and instant copulation occurred. Tandem pairs would break from the swarm with males usually detaching soon afterwards. At the Little River site, nuptial flights began later, almost at sunset and swarming occurred at much greater heights (ca. 40-60 m versus 20-35 m). Swarms of males were typically smaller (20-50 individuals). Eggs were deposited in flight at both sites as subspherical greenish masses. Newly hatched nymphs were identical to figures of Ide (1935b).

At both sites the developmental cycles were relatively complex. At Sinking Creek (Fig. 3a) there was an emergence of an overwintering brood of predinantly large-sized adults in May with another peak of smaller-sized individuals in mid-September. Adults

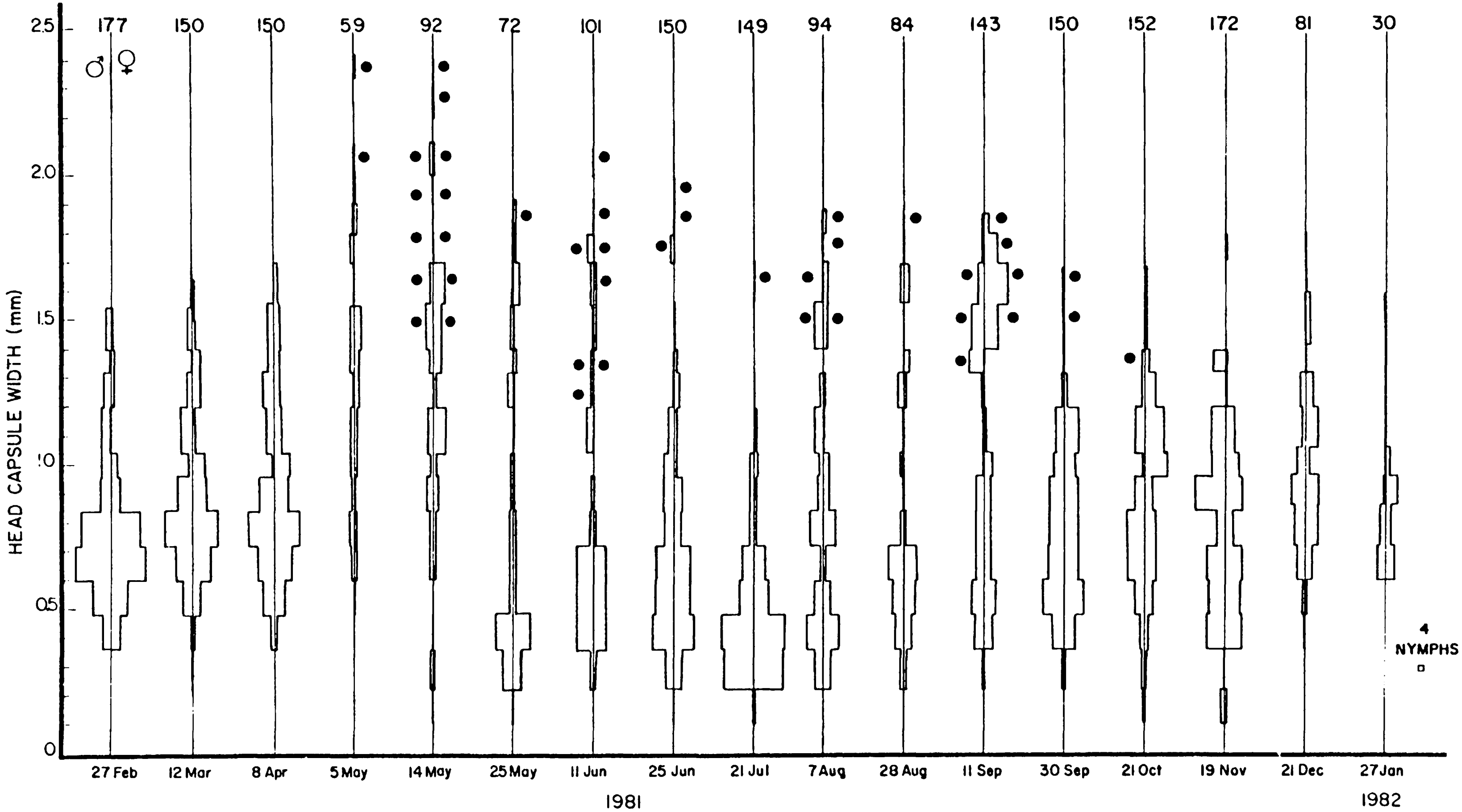


Fig. 3a. Size frequency distribution of head capsule widths of <u>Isonychia</u> <u>bicolor</u>. Sex could be determined for nymphs with head widths > 0.9 mm. Black dots denote nymphs with black wing pads; Sinking Creek.

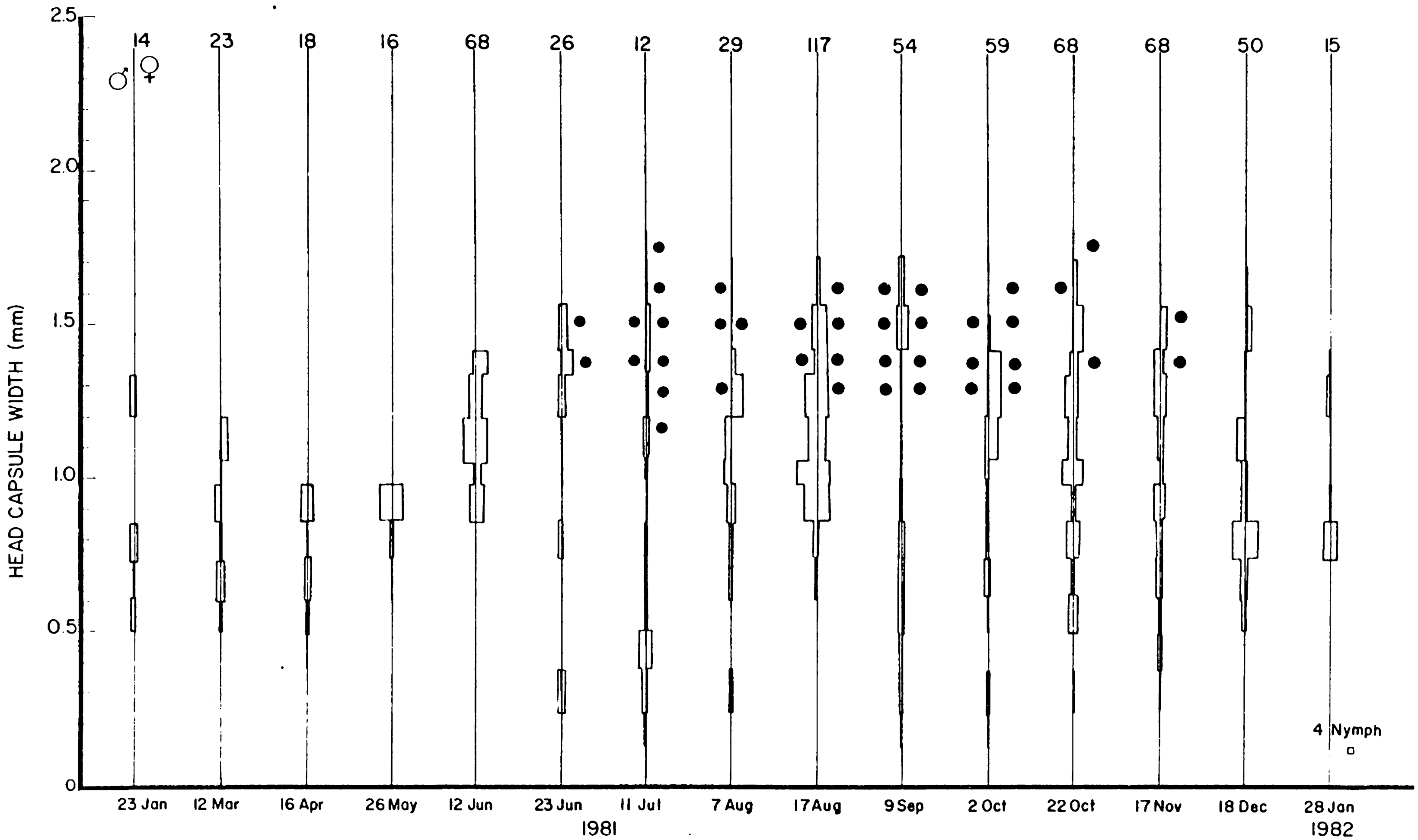


Fig. 4a. Size frequency distribution of head capsule widths of Isonychia bicolor. Sex could be determined for nymphs with head widths > 0.9 mm. Black dots denote nymphs with black wing pads; Little River.

Table 3. Seasonal variation of characters that have been commonly used to distinguish species of Isonychia (I. bicolor; Sinking Creek; 1981).

Date	Abdominal Color as Hue Value/Chroma of Munsell	Foretarsi Color	Body Length of Male Imago (mm)
15 May	10 red 3/4	light brown	15
18 May	2.5 yellow red 3/4	light brown	14
18 May	2.5 yellow red 3/4	whitish	15
18 May	10 red 3/4	light brown	16
18 May	10 red 3/4	light brown	15
26 May	7.5 red 3/4	light brown	15
26 May	10 red 3/4	whitish	16
27 May	5 yellow red 4/6	whitish	16
27 May	10 red 3/4	light brown	14
27 May	2.5 yellow red 3/4	light brown	16
10 June	2.5 yellow red 3/4	brown	14
10 June	7.5 red 2/2	brown	13
10 June	10 red 3/4	brown	11
10 June	10 red 3/4	brown	13
24 June	7.5 red 2/2	brown	14
10 July	2.5 yellow red 3/4	whitish	12
10 July	10 red 3/4	brown	11
10 July	10 red 3/2	whitish	10
22 July	2.5 yellow red 3/4	whitish	11
22 July	2.5 yellow red 3/4	brown	10
1 Aug	2.5 yellow red 3/4	whitish	11
1 Aug	2.5 yellow red 3/4	dark brown	10
1 Aug	10 red 3/4	brown	10
1 Aug	10 red 3/4	brown	10
1 Aug	10 red 3/4	whitish	11
11 Sept	10 red 3/4	dark brown	11
12 Sept	2.5 yellow red 3/4	brown	11
12 Sept	10 red 3/2	brown	10
17 Sept	2.5 yellow red 3/4	dark brown	11
17 Sept	10 red 3/4	brown	11
2 Oct	10 red 3/4	dark brown	11
6 Oct	2.5 yellow red 3/4	dark brown	11
6 Oct	10 red 3/2	brown	11

Table 4. Seasonal variation of characters that have been commonly used to distinguish species of *Isonychia* (*I. bicolor*; Little River; 1981).

Date	Abdominal Color as Hue Value/Chroma of Munsell	Foretarsi Color	Body Length of Male Imago (mm)
20 May	2.5 yellow red 3/4	whitish	12
12 July	2.5 yellow red 3/4	brown	11
12 July	2.5 yellow red 3/4	whitish	11
20 July	2.5 yellow red 3/4	light brown	11
25 July	2.5 yellow red 3/4	whitish	11
25 July	2.5 yellow red 3/4	brown	11
4 Aug	2.5 yellow red 3/4	brown	11
4 Aug	2.5 yellow red 3/4	brown	12
6 Aug	2.5 yellow red 3/4	brown	10
6 Aug	2.5 yellow red 3/4	light brown	11
6 Aug	2.5 yellow red 3/4	brown	11
19 Aug	2.5 yellow red 3/4	brown	11
19 Aug	2.5 yellow red 3/4	dark brown	12
19 Aug	10 red 3/4	brown	11
26 Aug	2.5 yellow red 3/4	brown	11
26 Aug	10 red 3/4	brown	11
9 Sept	2.5 yellow red 3/4	brown	12
11 Sept	2.5 yellow red 3/4	brown	12
12 Sept	10 red 3/4	whitish	9
13 Sept	2.5 yellow red 3/4	brown	12
13 Sept	2.5 yellow red 3/4	light brown	11
17 Sept	2.5 yellow red 3/4	whitish	10
17 Sept	2.5 yellow red 3/4	brown	11

or mature nymphs were present from May to October. The overlapping of generations was produced by the overwintering of various different developmental stages. Little growth occurred from December to March. The largest-sized overwintering nymphs (usually females) emerged first (early May) followed by a continuation of gradually smaller-sized adults from June to early October. Increasing water temperatures resulted in faster development and smaller-sized adults during these months. Eggs laid during May to early July produced the September peak. Eggs laid by the summer and fall emerging adults formed the overwintering population. Eggs from reared female imagoes were inseminated artificially as described by Sweeney (1978). Eggs from a single female hatched over a period of 21-56 days at both sites.

These observations agree with those reported by Sweeney (1978) for a Pennsylvania population of _I. bicolor_. However, the White Clay Creek population did have more divergent generations with apparently little or no overlap. His study documented that developmental rates are correlated with temperatures.

The larger spring emerging adults at Sinking Creek were variable in abdominal color intensity, (Table 3) with tarsi whitish to shaded with light brown. The later emerging individuals were also variable in abdominal color (Table 3) and had foreleg tarsi shaded with brown to dark brown and usually darker wing venation. (In Tables 3-4, a color using the Munsell system (H V/C), hue is written first followed by a fraction with the numerator indicating the value and the nominator the chroma. All hues at both sites were either reds or yellow reds of 2.5 YR, 5 YR, 7.5 R, to 10 R). Spieth (1938) indicated that body coloration is not chitinous in origin but originates from the underlying tissues. Apparently temperatures have an effect on the pigments in these tissues. Using previously available keys, original descriptions, and type material, the adults and nymphs of the Sinking Creek spring emerging adults could easily be determined as _I_. _bicolor_, _I_. _christina_, or _I_. _sadleri_, and the summer/fall-emerging adults as _I_. _harperi_, and the late fall individuals were very similar to _I_. _matilda_. At all times there were individuals that were intergrades of all of the above species.

At the Little River, (Fig. 4a), there were no discrete generations detectable. Adults or mature nymphs were collected from June to mid-November. Adults exhibited little size variation or color variability throughout the year apparently because of warmer water temperatures (Fig. 2a) that extended over a longer period of time. Water temperatures remained above 15°C from May to October. At the Sinking Creek site water temperatures were above 15°C only from June to September. Sweeney (1978) indicated that *I. bicolor* nymphs showed little growth below 15°C and no emergence at or below 10°C. Greatest emergence at the Little River occurred from late August to mid-September. Adults at this site were rather uniform in abdominal color (Table 4) and usually had whitish or brown foretarsi. These could be assigned to either *I. bicolor* or *I. harperi*.

Discussion:

Isonychia bicolor was originally described from a single female imago by Walker (1853) from the Albany River, Ontario, Canada. It remained virtually unrecognizable for over 75 years because of Walker's vague description and the fact that the type was a female subimago. Needham (1905) described C. albomanicata from all stages from Ithaca, New York. McDunnough (1931) reviewed the known eastern North American species of Isonychia and considered C. albomanicata a synonym of I. bicolor because of the occurrence of only one variable species in eastern North America. Traver (1932, 1935) did not accept McDunnough's rationale and considered I. albomanicata a valid species. Spieth (1940) critically studied the holotype of I. bicolor and confirmed McDunnough's previous conclusions. The type of I. bicolor was not examined in this study but examination of much material of the bicolor group from eastern Canada and eastern United States clearly substantiated McDunnough's (1931) and Spieth's (1940) previous conclusions.

Isonychia bicolor usually has at least two generations a year throughout much of its range. There is a larger-sized overwintering spring emerging generation usually followed by a faster developing and smaller-sized summer or fall generation. There is much more overlapping of generations in lower elevations and more southern latitudes. The larger-sized adults emerging from the overwintering brood at medium to usually represented the larger-sized and early season medium to high elevations had been previously usually identified as _I_. _sadleri_. _Isonychia_ _christina_ is only a smaller simple color variant of _I_. _bicolor_. Members of the smaller-sized, often darker, summer-and fall-emerging brood had been usually previously identified as _I_. _harperi_. _Isonychia_ _harperi_ variants appear to be more common in medium to large streams at medium to high elevations. _Isonychia_ _matilda_ was the name previously applied to very dark variants emerging in late summer or fall from smaller streams at higher elevations. _Isonychia_ _circe_ was the name usually applied to the pale color variants from larger warm-water southeastern streams at low elevations. _Isonychia_ _fattigi_ is another darker and usually smaller form of _I_. _bicolor_, often predominating in medium size streams of lower elevations. The Florida records of _I_. _fattigi_ in Berner (1977) are not of that species but represent a new species of the _sicca_ group.

Isonychia _pacoleta_ is only known from the type specimens collected from the Pacolet River in North Carolina. Berner (1977) after extensive collecting of southeastern mayflies, listed nymphs from only one locality in Tennessee. These proved *I. bicolor*. Such a restricted distribution is not typical of *Isonychia* and cannot be explained in terms of geography. I reared adults from the type locality stream (Pacolet River) and these specimens were clearly referable to *I. bicolor*. Traver (1932) in her key to the North Carolina species of *Isonychia*, stated that the venation of *I. pacoleta* was dark brown. However, her original description and my examination of the types indicate that the venation is whitish. The penes of the types of *I. pacoleta* fall within the range of *I. bicolor*. On the basis of the above, *I. pacoleta* is also placed as junior synonym of *I. bicolor*.

There are four basic color forms of mature nymphs (see description of nymph). Form 1 usually predominates in the northeastern portion of the range of *I. bicolor* or often in cooler streams. Forms 3 and 4 are apparently more common at lower elevations in warmer streams. However it is not uncommon to collect all forms and intergrading forms from a single stream anywhere in the range of *I. bicolor* throughout one season.

All characters used by Traver (1932, 1934, and 1935) to distinguish *christina*, *circe*, *fattigi*, *harperi*, *matilda*, *pacoleta*, and *sadleri*, were found to be extremely variable and totally unreliable. Examination of large series of adults and nymphs, many reared or associated, from throughout eastern North America and data from life history studies clearly indicated that only one very variable species, *I. bicolor* was involved. Previous adult criteria such as body and wing length, abdominal color, foreleg tarsal color and venation color; and nymphal diagnostic characters such as antennal color, gill color, middorsal abdominal stripe, and tibial spine lengths, are all related to developmental periods of the populations involving geography, elevation, water temperature and stream size. The other synonyms represent size and color variants of *I. bicolor*.

Material:

Holotype M (parts on slide), *Isonychia albomanicata*, New York: Ithaca (CU); Holotype M, *Isonychia christina*, New York: Ithaca, Balch Hall light, 24 July 1931, C. N.

Hardy (CU# 1251)); Allotype F, same as Holotype (CU# 1251); Paratypes, 10 M, 2 F, same but 17 June 1931 (CU# 1251); 7 M, same but 24 July 1931 (CU# 1251); 16 F, same but 7 Aug 1932 (CU# 1251); Holotype M, Isonychia circe, Georgia: Chattahoochee River, Atlanta, 8 Aug 1932, P. W. Fattig (CU# 1252.1); Allotype F, same as Holotype (CU# 1252); Paratypes, 4 M, 4 F, same as Holotype but 4-10 July 1931 (2 M, 3 F CU# 1252); 2 M, 1 F CNC); 1 M, same as Holotype but 1 Aug 1931 (CU# 1252); 2 M, same as Holotype but 30 June 1932 (CU# 1252); 1 M, same as Holotype but 8 July 1932 (CU# 1252);; 2 F, 1 sub F, Alcova River, S. of Monroe, 12 Aug 1931, P. W. Fattig (CU# 1252); 2 F, Apalachee River, N of Monroe, 12 Aug 1931 (CU# 1252); Holotype M, Isonychia fattigi, Georgia: Swamp Creek, Dalton, 25 June 1931, P. W. Fattig (CU# 1254); Allotype F, same but June (CU# 1254); Paratypes, 1 M, 2 F, same as Allotype (1 F, CU# 1254, 1 M, 1 F, CNC); 2 F, Apalachee River, Monroe, 12 June 1931, P. W. Fattig (CU# 1254); Holotype M, Isonychia harperi, New York: St. Regis River, Ft. Jackson, 1-3 Sept 1932, L. Harper (CU# 1255); Allotype F, same as Holotype (CU# 1255); Paratypes, 1 M, same as Holotype (CU# 1255); 2 F, same as Holotype but 24 Aug 1932 (CU# 1255); 5 M, 2 F, same as Holotype but 30 Aug 1932 (3 M, 1 F, CU# 1255, 2 M, 1 F CNC); Holotyope M, Isonychia matilda, New York: Wild Flower Preserve, Slaterville, Aug 1932, J. G. Needham (CU# 1256.1); Allotype F (reared), same as Holotype but 11 Sept 1931, JRT (CU# 1256); Paratypes, 1 M, 1 F, same as Holotype (CU# 1256); 4 F (reared), same as holotype but 19 Sept 1931, JRT (CU# 1256); 6 M, 2 F, same but 21 Sept 1931 (5 M, 1 F, CU# 1256, 1 M, 1 F, CNC); 1 M, 1 F, 1 sub F, Wilseyville, Aug 1932, JRT (CU# 1256); Holotype M (reared), Isonychia pacoleta, North Carolina: Pacolet River, near Tryon, 15 July 1930, JRT (CU# 1091.1); Allotype F (reared), same as Holotype (CU# 1091.2); Paratypes, 1 sub M, 1 F, 1 sub F (reared), same as Holotype (CU# 1091); 1 M, 1 F (reared), same as Holotype but 17 July 1930 (CU# 1091); Holotype M, Isonychia sadleri, New York: Hatchery, Ithaca, 12 June 1932, W. O. Sadler (CU# 1258); Allotype F, same as Holotype (CU# 1258); Paratypes, 1 M, same as Holotype but 19 June 1931, (CU# 1258); 2 M, same as Holotype (1 M, CU# 1258, 1 M, CNC); 7 M, same as Holotype but on surface of pond (CU# 1258).

CANADA- Ontario, Britannia, 6 July 1931, L. J. Milne, 1 M (AMNH); Dornoch, 8 July 1930, W. E. Ricker, 1 F (ROM); East Creek, Horning Mills, 24 July 1928, F. P. Ide, 1 F (ROM); same but 11 June 1934, F. P. Ide, 1 M (ROM); same but 19 June 1934, F. P. Ide, 1 M (ROM); same but 16 July 1934, F. P. Ide, 5 M, 3 F (ROM); same but 21 July 1934, F. P. Ide, 3 M, 1 F (ROM); same but 30 July 1934, F. P. Ide, 1 M (ROM); same but 6 Aug 1934, F. P. Ide, 2 F (ROM); Glen Huron, 24 June 1930, F. P. Ide, 3 M (ROM); same but 20 June 1931, F. P. Ide, 2 F (ROM); same but 18 June 1932, F. P. Ide, 1 M, 1 Sub F (ROM); Moire River, Rt. 401 at Belleville, 10 Sept 1980, C. R. Parker, 2 N (VPI); Nipissing River, Algonquin Park, 3 Sept 1934, F. P. Ide, 1 F (ROM); Noisy River, Horning Mills, 21 July 1928, F. P. Ide, 1 M (ROM); O. Golf Club, 10 July 1924, J. McDunnough, 1 M (AMNH); Ottawa, 27 June 1938, C. H. Curran, 4 M (AMNH); Pine River, Horning Mills, 5 July 1928, F. P. Ide, 2 M, 1 F (ROM); Primrose, 10 July 1928, W. E. Ricker, 1 M, 3 F (ROM); Singhampton, 13 Aug 1930, W. E. Ricker, 1 Sub F (ROM); same but 4 Sept 1930, W. E. Ricker, 1 Sub F (ROM); same but 5 Sept 1930, F. P. Ide, 1 M (ROM); same but 12 Aug 1931, F. P. Ide, 1 F (ROM); Smoky Falls, Kapuskasing, 30 July 1935, F. P. Ide, 1 M, 1 F (ROM); Timagami, 10 Sept 1934, W. A. Brown, 2 M, 1 Sub F (ROM); Vaudrevil, 20 July 1932, F. P. Ide, 2 M (ROM); Ottawa, 6 July 1934, F. P. Ide, 1 M, 1 F (ROM); same but 25 July 1934, F. P. Ide, 1 M (ROM); Peel Co., Credit River, Erindale, 11 Aug 1976, T. Yamamoto, 1 N (ROM); Quebec, Aylmer, 3 Aug 1930, ? 3 M (AMNH); Cascades Point, 5 July 1930, G. S. Walley, 9 M (CNC); O. Golf Club, 20 Sept 1934, F. P. Ide, 1 M (ROM); St. Lawrence River, Montreal, 5 Sept 1934, HTS, 8 M, 14 F (AMNH); Renfrew Co., Eganville, ? 2 M (MCZ); United States- Connecticut: Saugatuck River, Redding, 10 June 1933, HTS, 1 M, 42 F (AMNH); Georgia: Chattahoochee River, Helen, 19 July 1945, P. W. Fattig, 3 M, 1 F (INHS); Sharpsburg, 2 June 1948, P. W. Fattig, 2 M, 1 F (UF); Cherokee Co., Etowah River, St. Rd. 861, 22 June 1971, W. L. Peters et al. 2 M (FAMU); White Co., Town Creek, 1.5 mi. off Rt. 115 nr. Cleveland, 8 July 1981, BCK, 4 M, 12 F (reared), 7 N (VPI); Illinois: Eddyville, 23 May 1946, Mohr and Burks, 1 M (INHS); Kankakee, 2 Aug 1938, Boesel and Burks, 1 M (INHS); same but 4 Aug 1938, Boesel and Burks, 4 M, 2 F (INHS); same but 16 Aug 1938, Ross and Burks, 1 M (INHS); Lusk

Creek, Eddyville, 15 May 1946, Mohr and Burks, 2 M (INHS); Oakwood, 24 July 1939, B. D. Burks, 1 M (reared) (INHS); Rock Island, 7 June 1939, Burks and Riegel, 1 M (INHS); Wilmington at light, 6 Aug 1947, Burks and Sanderson, 4 M, 1 F (INHS); Kankakee Co., 10 July 1925, T. H. Frison, 2 M (INHS); Pike Co., 26 May 1906, ? 1 M (INHS); Indiana: Spencer, McCormick St. Park, 4 June 1929, Gall, 13 F (AMNH); St. Joseph River, Elkhart, 7 Aug 1940, HTS, 2 M (AMNH); Harrison Co., Blue River, 1 mi. E White Cloud, 29 Aug 1971, W. P. McCafferty, 1 M, 1 F (PU); Martin Co., White River, at Hindostan Falls, 13 Aug 1974, A. V. Provonsha, 1 M, 2 sub M, (PU); Martin Co., White River, at Shoals, 7 June 1978, M. Minno et al., 2 M (PU); Massachusetts: Athol, 1 July 1935, HTS and Spence, 10 M, 49 F (AMNH); Maryland: New Windsor, Aug 19 ?, V. Argo, 3 M (CU); Michigan: Grand River, Lowell, 29 July 1927, ?, 2 M, 1 F (AMNH); Pine River, Alma, 28 July 1929, ?, 6 F (AMNH); White Cloud, 31 May 1940, ?, 1 M, 1 F (AMNH); Crawford Co., 8 Aug 1947, J. W. and F. Leonard, 39 N (UM); Ausable River, 5 May 1948, J. W. and F. Leonard, 4 N (UM); same but 2 July 1948, J. W. and F. Leonard, 1 Sub F (reared) (UM); same but 5 July 1948, J. W. and F.

Leonard, 3 M, 1 F (UM); same but at Rieth Haven, 5 July 1948, J. W. and F. Leonard, 1 M, 3 F (UM); same but at Rieth Haven, 15 July 1948, J. W. and F. Leonard, 1 M (UM); same but 15 July 1948, J. W. and F. Leonard, 2 M, 18 F (UM); same but 11 Sept 1948, J. W. and F. Leonard, 1 M, 12 F (UM); same but 19 June 1950, J. W. and F. Leonard, 1 M, 1 F (UM); same but 22 June 1950, J. W. and F. Leonard, 1 F (UM); same but 12 July 1950, J. W. and F. Leonard, 3 F (UM); same but 20 Sept 1950, J. W. and F. Leonard, 1 F (reared) (UM); Lake Co., Pere Marquette, 24 Aug 1947, J. W. and F. Leonard 6 M, 5 F (UM); Otsego Co., Pigeon River, Hdgts., 20 Aug 1949, R. J. Ellis 1 F (UM); Maine: Pinobscot Co., Orono, U. Maine, at light, 25 July 1979, T. M. Mingo 1 M, 2 F (TM) same but 28 July 1979, T. M. Mingo 1 M (TM) same but 30 July 1979, T. M. Mingo 2 M (TM) same but 3 Aug 1979, T. M. Mingo 1 F (TM) Minnesota: Mississippi River, Fridley, 10 June 1937, R. H. Daggy 1 M (UMN): Missouri: Big Springs St. Park, 17 June 1954, J. W. Green 1 M (CAS); Little Osage River, Lebanon, 19 June 1936, Voris and HTS 1 M, 5 F (AMNH); Christian Co., Finley Creek,, ca. 1 mi. E of Linen, 7 Oct 1979, D. M. Sullivan, 1 M, 1 F (PU); Mississippi Pike Co., LB, 1 M

(UF); North Carolina: Oconaluftee River, Cherokee Reser., 16 June 1979, S. Hiner, 1 F (VPI); Valle Crucis, 30 May 1935, L. C. Thomsen, 6 M (UU) same but 25 May 1936, JRT, 1 M (CNC); same but 27 May 1936, JRT, 1 M, 1 F (UU) Cherokee Co., Murphy, 26 July 1930, HTS, 12 M, 10 M (AMNH); same but 27 July 1930, HTS, 7 M, 15 F (AMNH); Guliford Co., Big Alamance Creek, Rt. 3336 at Rt. 1005, 23 May 1981, BCK, 5 M, 4 F (reared), 3 N (VPI); same but 15 Sept 1981, BCK, 18 M, 24 F (reared), 8 N (VPI); Macon Co., LB, 2 M, 1 F (UF); Macon Co., LB, 4 M, 1 F (UF); Swain Co., Bryson City, 30 July 1930, HTS, 2 M, 3 F (AMNH); same but 3 Aug 1930, HTS, 2 M, 3 F (AMNH); New Hampshire: Franconia, A. T. Slosson, 1 M, 1F (AMNH); New Jersey: Musconetcong River, Penwell, Washington, 30 June 1957, E. L. Mockford, 1 M, 2 F (INHS); Oakland, 16 Aug 1935, ?, 1 M (AMNH); New York: same but Wellington, 7 Sept 1934, HTS, 1 M, 3 F (AMNH); Beaverkill River, Beaverkill, 16 June 1935, HTS, 9 M, 4 F (AMNH); Esopus River, Shadaken, 15 June 1935, HTS, 6 M, 5 F (AMNH); Fall Creek,, Ithaca, 3 N (CU) Hackettstown 3 June 1935, HTS, 2 M (AMNH); Hanock, East Branch Delaware River, 23 July 1935, H. K. Towns, 3 N (UMN); Ithaca, 11 June 1935, H. K. Towns, 1 M (UMN);

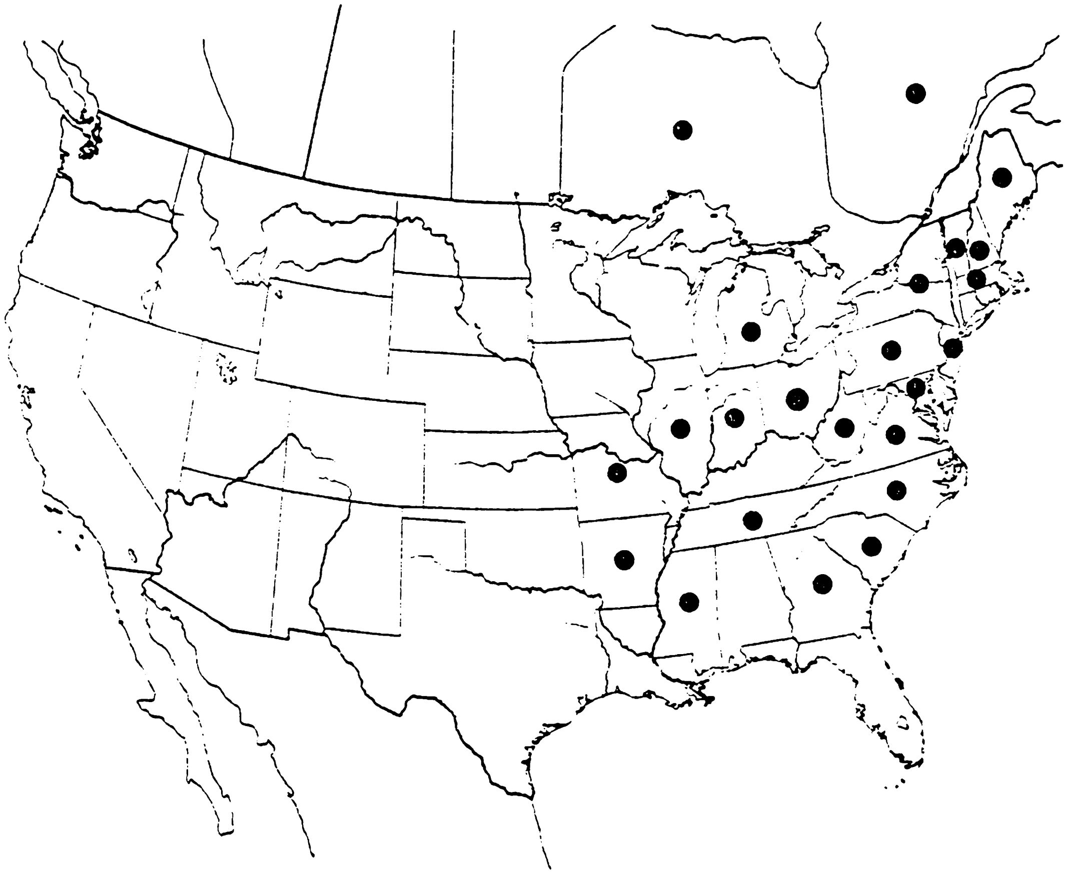
Lexington, 15 June 1935, HTS, 2 M, 3 F (AMNH); N. Pharsalia, Canasawacta Creek, 23 Aug 1935, H. K. Towns, 1 N (UMN); Niagara Falls, 21 July 1933, A. l. Melander, 13 M, 19 F (AMNH); Sacandasa River, Short Island, 27 June 1910, N. Banks, 1 M (MCZ); Sloatsburg, 4 June 1933, HTS, 32 M, 11 F (AMNH); same but 25 May 1935, HTS, 1 M (AMNH); same but 29 May 1935, HTS, 1 M (AMNH); Tuxedo, 4 June 1932, HTS, 4 M (AMNH); Pennsylvania: Analomink, 25 June 1938, Jennings, 2 M (AMNH); Williamsport, 17 June 1948, W. Bennett, 1 M (INHS); Cocalico Creek,, NW of Denver, 23 Aug 1948, J.W.H.R. 15 N (ANSP); Devon, at light 7 July 1964, SSR, 9 M, 3 F (ANSP); Ridley Creek,, rt. Branch, Rt. 352, 8 July 1959, SSR, 8 N (ANSP); Chester Co., East Br. of White Clay Creek,, Rt. 926, 23 Sept 1968, J. W. Richardson, 4 M, 3 F (ANSP); same but 11 Sept 1969, J. W. Richardson, 1 M (ANSP); same but 25 June 1970, J. W. Richardson, 2 M (reared) (ANSP); same but 27 June 1970, J. W. Richardson, 1 M (reared) (ANSP); same but 12 June 1967, J. W. Richardson, 4 M (UU) same but 23 Aug 1966, J. W. Richardson, 1 M (UU) South Carolina: Lawrence Co., Ware Shoals 29 June 1930 , HTS 2 M (AMNH); Tennessee: Knoxville, 10 June 1891, ?, 2 F (INHS); same but 11

June 1891, ?, 1 M, 3 F (INHS); Cheatham Co., 2 July 1954, S. W. Edwards, 1 M, 1 sub M (UF); Greene Co., Cummins Branch at Paint Creek, 11 Sept 1981, BCK, 1 F (reared) (VPI); Overton Co., Roaring River, 5 May 1976, BCK and J. Foster, 1 M (reared) (VPI); same but 8 May 1976, BCK, 1 M, 1 F (reared) (VPI); Putnam Co., Blackman's Fork, Cummings Falls, 17 March 1976, BCK, 17 N (VPI); Unicoi Co., Erwin, 13 June 1960, LB, 1 M (UF); Virginia: Fall Church, N. Banks, 1 F (MCZ); Bath Co., Back Creek, Blowing Springs, St. Rt. 39,10 Sept 1979, BCK, 5 F (VPI); Jackson River, Co. Rt. 603, 11 Sept 1979, BCK, 1 M, 1 F (VPI); Bedford Co., N. Boone Farm, 10 July 1980, J. Despins, 2 M (VPI); Bland Co., Wolf Creek, St. Rt. 61, 10 June 1978, BCK, 1 M (VPI); Clear Fork Creek, St. Rt. 61, 10 June 1978, BCK, 1 M (VPI); Botetourt Co., Craig Creek, 1/4 mi. from Co. Rt. 705, 28 May 1977, BCK, 6 M, 10 F (VPI); Carroll Co., New River, Co. Rt. 606, 11 June 1980, BCK, 1 M (reared) (VPI); New River, Fries, 25 July 1976, J. Kennedy, 1 M (VPI); same but 2 Aug 1976, C. R. Parker, 1 M, 5 F (VPI); Craig Co., Barbour's Creek, 27 May 1977, R. E. Jenkins, 2 M, 2 F (VPI); Potts Creek, Co. Rt. 600, 26 June 1977, BCK, 15 M, 6 F (VPI); John's Creek, St. Rt.

311, nr. junction Co. Rt. 611, 30 June 1978, BCK, 2 M, 2 F (VPI); Culpeper Co., Hazel River, off Co. Rt. 707, 7 Sept 1980, BCK, 3 M, 5 F (reared) (VPI); same but 3 July 1981, BCK, 26 M, 19 F (reared) (VPI); Fairfax Co., Bull Run Creek, .25 mi. W of Co. Rt. 615, 14 Aug 1980, 3 M, 1 F (reared), 2 N (VPI); Floyd Co., Little River Co. Rt. 615, 21 April 1977, BCK, 1 M (reared) (VPI); same but 27 May 1977, BCK, 1 M, 5 F (VPI); Giles Co., Big Walker Creek,, Co. Rt. 622 29 Sept 1977, J. R. Voshell, 1 M (VPI); same but New River, Glen Lynn, 8 July 1980, R. Lechteitner, 3 M (reared) (VPI); Pembroke, at light, 14 July 1977, P. K. Powell, 19 M (VPI); same but 16 July 1977, BCK, 11 M, 3 F (VPI); same but Rt. 460, at light, 21 May 1977, P. K. Powell, 1 M, 3 F (VPI); Sinking Creek, St. Rt. 42, Newport Park, 29 April 1977, BCK, 1 F (reared) (VPI); same but 15 May 1977, 4 M, 2 F (VPI); same but 18 May 1977, 8 M, 2 F (VPI); same but 20 May 1977, 1 M (reared) (VPI); same but 26 May 1977, 17 M, 2 F (VPI); same but 10 July 1977, 10 M, 1 F (VPI); same but 29 May 1978, B. Stauffer, 1 M (VPI); same but junction of Co. Rt. 700 and 604, 24 June 1978, BCK, 1 M (VPI); same but St. Rt. 42, Newport Park, 1 Aug 1980, 3 M, 6 F (reared), 1 N

(VPI); same but 24 May 1981, 1 F (reared), 2 N (VPI); same but 27 May 1981, 1 M, 4 F (reared) (VPI); same but 10 June 1981, 6 M, 4 F (reared), 1 N (VPI); same but 22 July 1981, 2 M, 2 F (reared) (VPI); same but 30 Aug 1981, 2 F (reared) (VPI); same but 11 Sept 1981, 4 M, 4 F (reared) (VPI); same but 14 Sept 1981, 5 F (reared) (VPI); same but 17 Sept 1981, 3 M, 2 F (reared) (VPI); same but 2 Oct 1981, 1 M, 1 F (reared) (VPI); same but 6 Oct 1981, 2 M, 5 F (reared) (VPI); same but 14 Oct 1981, 1 F (reared) (VPI); Giles Co., Stony Creek,, Co. Rt. 635, 13 July 1977, J. R. Voshell, 1 M, 2 F (VPI); Walker Creek,,Co. Rt. 622, 14 July 1978, BCK, 1 M, 4 F (VPI); Grayson Co., New River, Co. Rt. 606, junction with Co. Rt. 721, 5 June 1980, BCK, 3 M (reared) (VPI); same but 11 June 1980, BCK, 1 M, 3 F (reared) (VPI); New River, Co. Rt. 640, 21 Sept 1981, BCK, 3 M, 12 F (reared) (VPI) same but Co. Rt. 678, 23 Sept 1981, BCK, 2 M, 5 F (reared), 3 N (VPI); Wilson Creek, Rt. 58/ Rt. 16, near Co. Rt. 796, 24 Sept 1981, BCK, 1 M, 1 F (VPI); Fox Creek, Co. Rt. 603, 24 Sept 1981, BCK, 4 M, 3 F (VPI); Hanover Co., North Anna River, Falls, 27 May 1978, BCK, 3 M (VPI); same but 2 July 1977, BCK, 3 M (VPI); same but 4 Aug 1977, 5 M, 4 F, BCK (VPI); same but 18 Aug 1977, 12 M, 6 F, BCK (VPI); same but 14 Sept 1977, 1 M, 1 F, BCK (VPI); same but South Anna River, Co. Rt. 657, 5 July 1977, BCK, 2 M, 3 F (VPI); same but 4 Aug 1977, BCK, 2 M, 1 F (VPI); same but 14 Sept 1977, BCK, 1 M, 1 F (reared) (VPI); Henry Co., Smith River, St. Rt. 57, junction Co. Rt. 698, 23 Oct 1978, BCK, 1 M, 1 F (VPI); Montgomery Co., Little River, Co. Rt. 787, 25 July 1980, BCK, 4 M, 4 F (reared), 1 N (VPI); same but 4 Aug 1980, 2 M (reared), 12 N (VPI); same but 6 Aug 1980, 5 M, 11 F (reared) (VPI); same but 9 Sept 1980, 2 M, 1 F (reared) (VPI); same but 13 Sept 1980, 2 M, 1 F (reared) (VPI); same but 15 Sept 1980, 1 F (reared) (VPI); same but 20 May 1981, 1 M (reared) (VPI); same but 24 June 1981, 2 F (reared) (VPI); same but 12 July 1981, 2 M, 3 F (reared) (VPI); same but 20 July 1981, 2 M, 1 F (reared) (VPI); same but 7 Aug 1981, 1 M, 7 F (reared) (VPI); same but 19 Aug 1981, 4 M, 1 F (reared) (VPI); same but 26 Aug 1981, 2 M, 4 F (reared) (VPI); same but 11 Sept 1981, 10 M, 14 F (reared), 8 N (VPI); same but 14 Sept 1981, 3 M, 6 F (reared), 1 N (VPI); same but 17 Sept 1981, 2 M, 2 F (reared) (VPI); same but 5 Oct 1981, 1 F (reared) (VPI); Mt. Tabor, at light, 1 Aug 1980, C. R. Parker, 1

M (VPI); New River McCoy-Longshop, 21 June 1981, BCK, 1 M (reared) 1 N (VPI); New River, McCoy Falls, 29 May 1979, Meador, 1 M, 1 F (VPI); New River, McCoy, 21 June 1979, K. Cannon, 7 M, 1 F (VPI); North Fork Roanoke River, Co. Rt. 603, 19 May 1980, M. Spencer, 2 M, 2 F (reared) (VPI); Tom's Creek, Co. Rt. 655, 29 May 1978, BCK, 2 M (reared) (VPI); same but 25 May 1978, BCK, 1 M (reared) (VPI); same but 19 April 1977, BCK, 1 F (reared) (VPI); VPI and SU Campus, 26 June 1981, BCK, 1 M (VPI); Nelson Co., South Fork Tye River, St. Rt. 56, Crabtree Rec. Area, 12 Sept 1977, 1 M, 11 F (reared) (VPI); Orange Co., Mine Run, off Co. Rt. 715, 16 July 1981, BCK, 6 M, 7 F (reared), 8 N (VPI); Rapidan River, off Co. Rt. 715, 16 July 1981, BCK, 14 M, 16 F (reared), 6 N (VPI); Radford New River, Radford Park, 11 Sept 1976, BCK, 2 M (VPI); Rappahannock Co., Hughes River, Co. Rt. 707, 7 Sept 1980, BCK, 1 M, 2 F (reared) (VPI); same but 7 Sept 1980, BCK, 1 F (reared) (VPI); Russell Co., Clinchfield, 1 Aug 1939, Rehn and Rehn, 1 M (ANSP); Shenandoah Co., North Fork Shenandoah River, Co. Rt. 707, 15 June 1971, E. W. Surber, 2 M, 3 F (VPI); Smyth Co., Big Laurel Creek, Co. Rt. 603, 24 Sept 1981, BCK, 1 M, 1 F (VPI); Spotsylvania Co., Catharpin Run, Co. Rt. 608, 15 July 1980, BCK, 2 M, 7 F (VPI); Rappahannock River, Co. Rt. 618, 14 July 1980, BCK, 7 M, 5 F (VPI); same but 15 July 1981, BCK, 38 M, 26 F (reared) (VPI); Warren Co., Shenandoah River, Front Royal, at light, 14 Aug 1980, BCK, 1 M (VPI); Washington Co., Tumbling Creek, Co. Rt. 747, 29 Aug 1979, BCK, 3 M, 4 F (VPI); Straight Branch, St. Rt. 58, nr. Feathercamp Branch, 25 Sept 1981, BCK, 1 M, 8 F (reared) (VPI); West Fork of Wolf Creek, Hayters Gap, St. Rt. 80, 25 Sept 1981, BCK, 2 M, 1 F (VPI); Vermont: Tabor Brook, Peru, 2 July 1937, HTS, 1 M (AMNH); West Virginia: Hampshire Co., Cacapon River, Rt. 50, 16 July 1980, BCK, 11 M, 12 F (VPI); Pocahontas Co., Sitlington Creek, Rt. 92 and Rt. 28, at Dunmore, 12 Aug 1981, BCK, and R. F. Kirchner, 3 M, 1 F (reared), 5 N (VPI);



Map 1. Distribution of I. bicolor (Walker). The black dot only denotes that specimens have been examined from the state. See records under "Material" for exact localities.

Isonychia (Isonychia) rufa

McDunnough

Figs. 2, 37, 53, 100, 101

Isonychia rufa McDunnough, 1931: 162. Type locality: Davenport, Iowa. M, F, Type deposition: (M) CNC; Traver, 1935: 495; Daggy, 1945: 387; Burks, 1953: 112.

Male Imago:

Body: length 9-14 mm, forewings 8-13 mm.
Head: Eyes purplish gray with dorsal portion separated by lighter transverse bands; ocelli whitish; ocellar elevations blackish. Blackish spot between compound eye and scape. Antennal scape and pedicel brownish, flagella whitish.
Thorax: Mesonotum light reddish-brown to orangish, mesoscutellum darker brown; metathorax dark brown. Pleura light reddish-brown, membranes with purplish tinge. Prothoracic leg dark reddish-brown, femur often yellowish-brown basally, tibia sometimes darker, tarsi yellowish to light brown, each segment brownish apically; meso- and metathoracic legs yellowish, tarsi and claws often tinged with brown. Wings hyaline with

all veins whitish to light yellow, forewings with whitish stain in stigmatic area, stigmatic cross usually anastomosed.

Abdomen: Terga bright red to reddish orange brown; terga 1-9 with purplish black bands on posterior margins, occasional bands obscure or interrupted medially; terga 1-9(8) with black spot or streak just above pleural fold at posterolateral edge. Sterna light reddish-brown to yellowish orange; sterna 1-9 with whitish midventral ganglionic regions. Caudal filaments whitish to yellowish, few basal articulations yellow to reddish. Forceps yellowish-brown, first segment of forceps often as wide as long (Figs. 2, 100-101).

Female Imago:

Body: length 10-14 mm, forewings 9-13 mm.

Head: Yellowish brown to orangish; ocelli whitish or grayish; ocellar elevations blackish. Posterolateral angles of occiput blackish; a blackish bar or spot below compound eye and scape. Antenňae brownish or yellowish.

Thorax: Mesonotum light reddish-brown to reddish-yellow, mesoscutellum tinged with brown; metanotum brown. Pleura light yellowish-brown, membranes tinged with brown or purple. Prothoracic leg dark reddish-brown, femur yellowish brown basally, tarsi yellowish, each segment brownish apically; meso- and metathoracic legs whitish or yellowish, tarsi often tinged with brown. Wings hyaline with all veins whitish to yellowish; stigmatic region of forewing stained with whitish, crossveins anatomosed.

Abdomen: Terga light reddish-brown to yellowish-orange; terga 1-9 with purplish black bands on posterior margins; terga 1-9 with blackish spot or dash just above pleural fold at posterolateral edge; terga 8-10 often yellowish. Sterna yellowish-brown to reddish-yellow; sterna 1-9 with whitish midventral ganglionic regions. Caudal filaments whitish to yellowish. Subanal plate deeply emarginate.

Egg: Typical of subgenus, terminal knobs of coiled threads often triangular (Fig. 53).

Nymph:

Body: length 10-14 mm.

Head: Light yellowish-brown to brown with whitish or very light yellow coronal stripe. Antennae whitish or yellowish, often tinged with brown.

Thorax: Nota yellowish-brown with whitish or yellowish middorsal stripe; pronotum with 2 pairs of submedian crescentric or often bar-like whitish spots; small whitish to yellowish spots and streaks anterior and lateral of mesothoracic wing pads. Legs yellowish-brown to yellowish with brownish marks forefemora yellowish with 2 submedian brownish bands, tibia whitish or yellowish usually with a median brown transverse band, tarsi yellowish with a subbasal brown transverse band; tarsi claws with 5-11 marginal denticles. Procoxal gill a tuft of multibranched purplish filaments.

Abdomen: Terga 1-9 yellowish-brown to light reddish-brown occasionally with anterior and posterior darker brown transverse bands; terga 1-9 with a yellowish middorsal stripe, often faint or apparently absent, stripe often margined laterally by whitish submedian streaks; terga 1-8(9) with a whitish or yellowish median spot near lateral margin; terga 10 brown posteriorly, yellowish anteriorly. Sterna yellowish-brown to light reddish-brown; sterna 1-9 with anterolateral brownish spot; sterna 1-9 usually with 2 or 3 whitish or yellowish submedian dots. Gill lamella with a large diffuse purplish spot; median sclerotized ridge brownish; fibrillar portion purplish. Caudal filaments yellowish-brown to reddish-brown, darker brown basally, each filament with a broad dark brown submedian band, blackish band at tip, between these two bands filaments yellowish to whitish.

Diagnosis:

Isonychia rufa may be distinguished from all other species of the *bicolor* group by the following combination of characters. In the male imago: (1) forewings hyaline, venation whitish to light yellowish, (2) penes dorsally with a relatively prominent basal dome-like swelling, forming lateral and apical ridges, (3) abdomen bright reddish to reddish orange brown, and (4) stigmatic crossveins usually anastomosed.

The nymph is extremely similar to that of the sympatric *I. bicolor*. The nymphs usually can be separated by having the ventral apical cleft of the mesothoracic femur (at least on one side) with 5 or less stout marginal spines (Fig. 37). However, some individuals may have 6-7 spines, therefore a series of nymphs must be examined. Very mature nymphs of I. rufa are often light yellowish-brown with pale marking compared to the darker brown to reddish-brown nymphs of I. bicolor.

Discussion:

Isonychia rufa is a midwestern species ranging from Manitoba south to Okalahoma. Daggy (1945) described the nymph, noting the variability commonly encountered with Isonychia nymphs. Since nymphs of I. bicolor and I. rufa are so similar, nymphs should be reared for positive identification.

The records of I. rufa mentioned by Traver (1935) from New Windsor, Maryland were typical I. bicolor. The specimens from Mississippi were not available and considered here to be doubtful. One of the Mississippi records of I. rufa listed by Berner (1977) (Pike County) was examined and proved to be I. bicolor.

Biology:

Apparently _I_. _rufa_ is a species common in larger streams and rivers of the Mississippi drainage. Adults have been collected from April to September. McCafferty and Provonsha (1978) reported _I_. _rufa_ common in the Ozark-Quachita area of Arkansas, recording adults from May to late July.

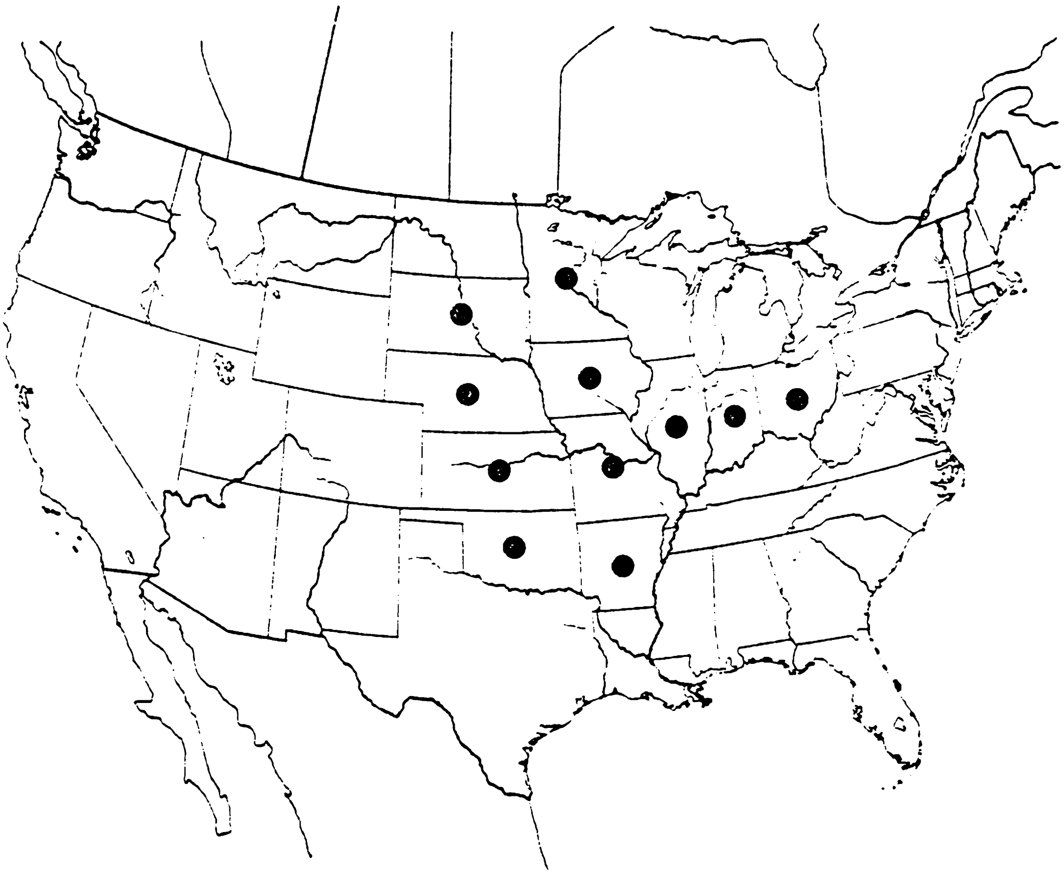
Material:

Paratype M, Iowa: Pleasant Valley, 4 July ?, G. S. Walley (CNC# 3251); Paratype M, Kansas: Douglas Co., Lawrence, 31 July 1930, L. W. Brown (INHS).

Arkansas: Benton Co., 15 June 1966, B. F. Jones, 1 M (FAMU); Drew Co., Fire Tower, approx. 15 mi. SE of Monticello on Hwy. 35, I. Brown, 2 M (FAMU); Montgomery Co., Little Missouri River at Alberst Pike Recreation Area, 30 May 1974, W. P. McCafferty et al., 1 M, 1 F (reared) (PU); Washington Co., 8 June 1964, B. F. Jones, 2 M (FAMU); same but 11 June 1964, 2 F (FAMU); same but 6 Aug 1964, L. O. Warren, 1 M (FAMU); same but 11 June 1966, 7 M (FAMU); Illinois: Apple, R. C. S. P. Sweeping, 3 July 1946, Burks and Sanderson, 1 M (INHS); Aurora, 9 July 1907, 2 M, 1 F (INHS); same but at light, 17 July 1927, Frison et al., 7 F (INHS); Freeport, at light, 4 Aug 1948, Burks and Stannard, 3 F (INHS); Kankakee, 2 Aug 1938, Boesel and Burks, 1 M (INHS); same but 9 July 1948, Ross and Burks, 1 F (INHS); Monmouth, 23 June 1948, L. J. Stannard, 1 M (INHS); Oakwood, 14 July 1939, Burks and Riegel, 1 M (INHS); Omarga, at light, 9 July 1948, Ross and Burks, 1 F (INHS); Oregon, 4 July 1946, Burks and Mohr, 6 M, 2 F (INHS); Peoria, 13 July 1940, F. F. Hasbrouk, 1 M (INHS); same but 1 July 1941, 1 M (INHS); Quincy, 8 June 1939, Burks and Riegel, 1 M (INHS); Sangamon River, White Heath, 5 Aug 1939, Ross and Riegel, 1 M (INHS); Savanna, 20 July 1927, T. H. Frison, 2 F (INHS); St. Charles, at light, 8 July 1948, Ross and Burks, 2 M (INHS); Urbana, at light, 5 July 1907, ?, 2 M, 1 F (INHS); Wilmington, at light, 6 Aug 1947, Burks and Sanderson, 7 M, 3 F (INHS); W. Chicago, 9 July 1948, Ross and Burks, 1 F (INHS); Indiana: Benton Co., Mud Creek at St. Rd. 71, 2.5 mi. N of Freeland Park, 14 July 1976, Provonsha et al., 1 M (reared) (PU); Stake Co., Yellow River at Knox, 14 July 1976, A. V. Provonsha and M. Minno, 3 M, 12 F (reared) (PU); Iowa: Red Oak, 28 July 1946, H. H. Ross, 2 M, 4 F (INHS);

Kansas: Douglas Co., 5 May 1921, W. J. Brown, 1 M (UK); same but 12 June 1921, 1 M (UK); same but 14 June 1921, 3 M, 4 F (UK); same but 15 June 1921, 4 M, 4 F (UK); same but 16 June 1921, 1 F (UK); Wakarusa River at U.S. 59 Hwy. bridge, 25 July 1978, P. Liecht, 2 M, 2 F (reared) (PL); Lawrence, electric light, 8 June 1922, W. J. Brown, i F (UK); same but July 1929, 17 M, 13 F (CNC); same but 23 June 1931, L. W. Brown, 1 m (AMNH); same but 16 Sept 1931, 1 m (AMNH); Ellsworth Co., 12 July 1923, R. H. Beamer, 1 F (UK); Phillips Co., 1940', 30 Aug 1912, F. X. Williams, 1 M (UK); Pottawatomie Co., 7 July 1955, McReynolds, 1 F (UK); Riley Co., Manhattan, at light, 23 May 1952, H. E. Evans, 3 M, 3 F (FAMU); Saline Co., 13 July 1923, W. B. Whitlow, 2 F (UK); same but R. H. Beamer, 2 F (UK); Minnesota: Anoka Co., Fridley, 28 Sept 1938, R. H. Daggy, 1 F (UMN); same but 25 July 1939, 1 F (UMN); Blue Earth Co., Mankato, at light, 13 Aug 1938, R. H. Daggy, 2 M, 2 F (UMN); Blue Earth River, Rapidan, 18 Aug 1938, J. H. Mohr, 1 M (reared) (INHS); Climax, 27 July 1937, R. H. Daggy, 2 M (UMN); Hubbard Co., Park Rapids, 29 July 1938, D. G. Denning, 1 F (UMN); Martin Co., Fairmont, 27 July 1938, R. H. Daggy, 1 M (UMN); Minneapolis, at light, 12 July 1938, R. H. Daggy, 1 F (UMN); same but 14 July 1938, 1 M, 1 M (UMN); same but 15 July 1938, 2 M, 7 F (UMN); same but 20 July 1938, 2 M, 2 F (UMN); same but 15 Aug 1938, 1 F (UMN); same but 19 Aug 1938, 1 F (UMN); same but 29 June 1939, 1 M, 6 F (UMN); same but 31 June 1939, 3 M (UMN); same but 1 July 1939, 3 M (UMN); same but 13 July 1939, 1 M, 3 F (UMN); Morrison Co., Little Falls, at light, 10 July 1938, R. G. Denning, 4 M, 1 F (UMN); Park Rapids, 1 mi. S, 17 July 1939, 1 M (reared), 14 N (UMN); Pine Co., Pine City, at light, 15 Aug 1938, D. G. Denning, 8 F (UMN); Pine Island, at light, 25 June 1939, R. H. Daggy, 1 F (UMN); Rice Co., Faribault, 13 Aug 1938, R. H. Daggy, 1 M, 2 F (UMN); Rock Co., ? July 1938, at light, R. C. Stephens, 2 M, 1 F (UMN); Root River, Chatfield, 25 June 1939, R. H. Daggy, 21 N (UMN); Nebraska: Lincoln, at light, June, 1 F (INHS); same but August, 1 F (INHS); North Platt, 27 July 1946, H. H. Ross, 12 M, 6 F (INHS); Ohio: Marrow Co., Todds Fork, 7 Sept 1953, A. R. Gaufin, 1 M (FAMU); Ohio River, Cinncinnati, 15 June 1939, B. D. Burks, 4 M (INHS); Oklahoma: Broken Bow, 13 ? 1939, 2 M (AMNH); Rogers, 12 April 1946, H. H. Ross, 1 M (INHS); Sherwood, 27 June 1937, Standish and

Kaiser, 6 M, 4 F (AMNH); Tahlequah, 17 June 1939, 3 M (AMNH); South Dakota: Sioux Falls, Olivefalls at lights, 3 June 1938, ?, 3 M, 1 F (UMN);



Map 2. Distribution of I. rufa McDunnough.

Isonychia (*Isonychia*) *tusculanensis*

Berner

Figs. 3, 31, 43, 54

Isonychia tusculanensis Berner, 1948: 117. Type locality. Camp Creek, Greene County, Tennessee, M, F. Type deposition: (M) UM.

Male Imago:

Body: length 14-18 mm, forewings 13-17 mm.
Head: Eyes grayish with dorsal portion separated by lighter transverse bands; ocelli grayish; ocellar elevations dark brown to black. Blackish or brownish spot between compund eye and scape. Antennae brownish, distal portion of flagella grayish.
Thorax: Mesonotum brown; metanotum blackish brown. Pleura brownish, membranes yellowish tinged with red. Prothoracic leg dark brown, femur lighter brown or yellowish basally, tarsi light brown; meso- and metathoracic legs whitish to yellowish, tarsi tinged with brown distally, claws brownish. Wings hyaline with all veins whitish to light brown; apical half to third of forewing shaded with brown (Fig. 31), forewings with stigmatic crossveins anastomosed.

Abdomen: Terga dark reddish-brown to orangish brown; terga 1-9 with narrow purplish-black bands on posterior magins; terga 2-6(7) with narrow translucent bands posterior of blackish bands; terga 7-10 often lighter. Sterna reddish-brown to orangish-brown; sterna 1-9 with purplish bands on posterior margins. Caudal filaments brown to dark brown, lighter distally, articulations often very narrowly whitish. Forceps brown. Genitalia as Fig. 3.

Female Imago:

Body: length 15-20 mm, forewings 16-19 mm.
Head: Yellowish-brown; ocelli whitish or grayish; ocellar elevations blackish; dorsally with a pair of reddish stripe (fading after preservation). Posterolateral angle of occiput dark brown to black; a dark brown to black bar or spot below compound eye and scape. Antennae brownish, distal portion of flagella grayish.
Thorax: Mesonotum brown; metanotum dark brown; pleura brownish, membranes yellowish tinged with red. Prothoracic leg reddidh brown to dark brown, femur yellowish-brown to yellowish basally, tarsi light

brown. Wings hyaline with all veins reddish-brown, often darker at distal portion of wings; forewings without brown apical shading, stigmatic region with brownish stain, forewings with crossveins anatomosed. Abdomen: Terga dark reddish-brown to orangish; terga 1-9 with purplish-black bands on posterior margins; terga 8-10 often tinged with yellow. Pleural fold often margined with brown. Sterna reddish-brown to orangish; sterna 1-9 usually with purplish bands on posterior margins. Caudal filaments brown, distally distally lighter, articulations often narrowly whitish. Subanal plate deeply excavated.
Egg: Typical for subgenus, knob-terminated coiled threads denser in one hemisphere and absent in the other and absent in the other (Fig. 54).

Nymph:

Body: length 7-16 mm.
Head: Brown to yellowish-brown with whitish coronal stripe. Antennae whitish, scape and pedicel usually brown, basal flagellar segments often tinged with brown.

Thorax: Nota brown to yellowish-brown with a whitish middorsal stripe; pronotun with 2 pairs of whitish submedian concentric spots; small whitish often faint spots and streaks anterior and lateral of mesothoracic wing pads; a pair of faint whitish median spots on mesonotum, often absent. Legs brown with yellowish markings, forefemora brown with basal, median and apical spots or transverse bands, tibia whitish to yellowish-brown with median brown transverse band, tarsi yellowish to whitish with a wide basal brown transverse band; tarsal claws with 5-11 marginal denticles. Procoxal gills a tuft of multibranched purplish filaments.

Abdomen: Terga yellowish-brown to brown; terga 1-9 with a wide whitish or yellowish middorsal stripe, stripe bordered laterally by dark brown (Fig. 43); terga 1-9 either with a pair of faint submedian oblique streaks or a series of dots; terga 1-9 with a white spot on anterolateral margin; terga 10 yellowish-brown anteriorly, dark brown posteriorly. Sterna yellowish-brown; sterna 2-9 usually with a posterior midventral yellow or whitish streak or spot, often diffuse anteriorly; sterna 2-9 with a pair of submedian oblique yellowish streaks; sterna 2-7 with 2 pair of transverse yellowish spots, inner two often oblong. Gill lamella light gray to purplish, a brown diffuse spot often in distal margin; median sclerotized ridge brown; fibrillar portion purplish. Caudal filaments yellowish-brown, darker basally, each filament with a broad brownish transverse median band, a broad brownish or blackish band near tip, between these two bands, filaments usually whitish or light yellow.

Diagnosis:

Male imagoes of *I. tusculanensis* may be distinguished from all other Nearctic *Isonychia* by the uniform brownish shading of half to third of the forewing (Fig. 31). Females are very similar to the dark variants of *I. bicolor* and can not be separated consistently.

Nymphs are very similar to the sympatric *I. bicolor* and may be usually distinguished by the wide whitish or yellowish complete middorsal abdominal stripe bordered by dark brown (Fig. 43). Nymphs of *I. bicolor* which possess a wide complete middorsal abdominal stripe usually lack the bordering brown shading (Fig. 42).

Discussion:

Berner's (1948) description is excellent. *Isonychia tusculanensis* has only been collected in the Appalachian region of Tennessee and Virginia. This species has been collected in association with the very closely related *I. bicolor*.

Bajkova (1970) described *I. ussurica* from the Ussuri Basin, U.S.S.R. and distinguished it from all other Palearctic *Isonychia* by the distinctive brownish shading of half to third of the forewing. It apparently differs from *I. tusculanensis* in the form of the male genitalia and color of the caudal filaments.

Dr. T. E. Moore, Curator of Insects at the University of Michigan informed me that the Museum now only has the holotype, the allotype and other paratypes originally deposited being lost.

Biology:

This apparently uncommon species has been collected abundantly but very locally from several streams in southwestern Virginia. At one site, Yellow

Sulphur Springs (Montgomery County, VA), I. tusculanensis was the dominant mayfly. This first to second order stream in the Ridge and Valley Physiographic Province of Virginia had a good canopy of Eastern Hemlock (Tsuga canadensis (L.) Carr.), Yellow Popular, (Liriodendron tulipifera L.), and Sycamore (Platanus occidentalis L.). The stream varied from 1.5 to 2.0 m in width and averaged 10-25 cm in depth. Substrata was composed of pebble (16-64 mm) and cobble (64-128 mm) over exposed bedrock. At this site dissolved oxygen was usually above 99% saturation, pH averaged 8.2, conductivity averaged 80-169 umhos/cm, alkalinity averaged 271 mg/CCaCO3 and hardness averaged 287 mg/CaCO3. Water temperatures ranged from 2.5 (December or January) to 15 C (August). Other mayflies associated with I. tusculanensis at Yellow Sulphur Springs, a 19th century health spa, were Ephemerella rotunda Morgan, Ephemera guttulata Pictet, Stenacron interpunctatum (Say), and Habrophlebiodes americana (Banks).

Mature nymphs would swim to quiet and shallow eddies and sit quietly for a few minutes near a large rock, usually in the late morning. Several adults were observed to emerge. Mature nymphs of I. tusculanensis would usually swim to large projecting rocks and crawl up and out of the water, often 3-6 cm from the waters edge. Almost simultaneously the subimago would emerge. The newly emerged adult would sit near it exuvia for a few second to several minutes, and then fly high into nearby trees. Maximum emergence at this site was in mid-June.

This species was also extremely abundant in Station Spring Creek, Burkes Garden, in Tazeewell County, Virginia. This "canoeshaped" anticlinal, valley also lies in the Ridge and Valley Province of Virginia (Hoffman 1969) (elevation ca. 1430 m). Nymphs of I. tusculanensis were collected from headwaters areas down to 3rd - 4th order reaches of this creek. Substrata were mostly cobble (64-128 mm), pebble (16-64 mm) and some boulder (>256 mm) over exposed bedrock. Maximum water temperatures ranged from 12 C to 19 C. Adults and last instar nymphs at this site were collected from early June to late October, indicating possibly a typical bivoltine life cycle.

A large nuptial flight was observed at this site (mid-June). Just before dusk males formed large swarms of several hundred individuals over long fast riffles (maximum stream width 4.5 m) just below a mill pond. The rhythmic "dancing" was somewhat similar to Cooke's (1942) description. Females flying into the swarm would immediately be clasped, and the tandem pair soared out of sight. Swarming males would actively eluded capture by aerial nets. Females were observed ovipositing in riffles and quieter areas. Nymphal exuviae literally covered all projecting exposed surfaces of rocks at this site. Much smaller nuptial swarms were observed upstream (maximun stream width 1.5 m) with dead males littering the shallow eddies.

Numerous attempts were undertaken to recollect *I. tusculanensis* from its original type localities (Camp Creek and Frank Creek, Greene County, TN). These streams have undergone many perturbations since the late 1940's with heavy siltation and other pollution sources. The once diverse mayfly communities described by Wright and Berner (1949) have been eliminated or greatly reduced. Wright and Berner (1949) present excellent descriptions of these habitats and provide water chemistry data for many streams of eastern Tennessee where *I. tusculanensis* once was apparently common.

Kondratieff and Foster (1977) listed I. tusculanensis from Blount County, Tennessee, apparently the only recent record from Tennessee (see Berner 1977).

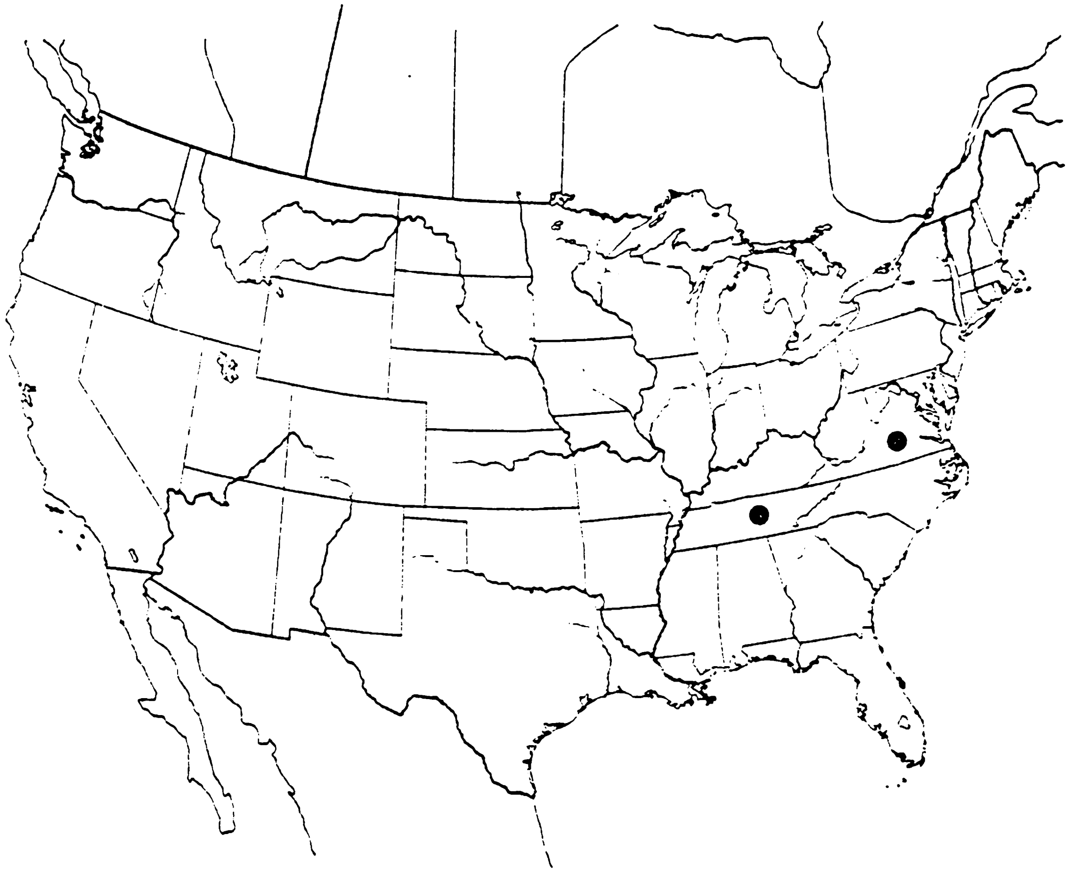
As an interesting note, males of I. tusculanensis were once collected swarming in company with Leptophlebia nebulosa (Walker) (Leptophlebiidae). Both species have apical regions of the forewings shaded with brown. The mating flight of L. nebulosa was not as vigorous as I. tusculanesis and males of the former species would come much closer to the waters surface on the downward leg of their flight pattern.

The male reared from Mill Creek, Virginia was a gynandromorph, having female type compound eyes. The male genitalia was typical. This is apparently the first report of gynandromorphism in Isonychia (Soldan and Landa 1981).

Material:

Holotype M, Tennessee: Greene Co. Camp Creek, 4 June 1947, M. Wright (3059.2) (UMI) Paratypes, 1 M, same but 10 June 1947 (3058.2) (UF); 1 F, same but 28 May 1946 (2019.1) (UF).

Tennessee: Blount Co., Pistol Creek, Maryville, 26 May 1976, BCK, 1 M (FAMU); Greene Co., Frank's Creek, 1 May 1948, M. Wright, 1 M (CAS); Virginia: Giles Co., Sinking Creek, St. Rt. 42, Newport, 1 Aug 1980, BCK, 1 M (reared); Montgomery Co., Mill Creek, Co. Rt. 785, 26 April 1982, BCK, 1 M (reared); Wilson Creek, Yellow Sulphur Springs, 23 June 1979, BCK, 1 M (reared) (VPI); Yellow Sulphur Springs, 13 June 1981, BCK, 1 M, 1 F (reared) (UF); same, 3 M, 4 F (reared) (VPI); Tazewell Co., Station Spring Creek, Burkes Garden, 10 June 1978, BCK, 35 M, 18 F, 4 M (reared) (VPI); small spring, base of Station Spring Creek at MBC Ranch, Burkes Garden, 1 Sept 1979, BCK, 7 M, 4 F (VPI); Station Spring Creek, MBC Ranch, Burkes Garden, 21 Oct 1979, BCK, 2 M, 2 F (VPI);



Map 3. Distribution of *I. tusculanensis* Berner.

<u>Isonychia</u> (<u>Isonychia</u>) <u>velma</u>

Needham

Figs. 4, 26, 32, 34, 55, 56

<u>Isonychia</u> <u>velma</u> Needham, 1932: 273. Type locality: Putah Creek, California, M, F. Type deposition (M) CU; Traver, 1935: 499; Day, 1952: 38; Day, 1956: 91.

Male Imago:

Body: length 15-18 mm, forewings 14-16.5 mm.
Head: Eyes gray with ventral portion brownish; ocelli whitish gray; ocellar elevations dark brown. Antennae brown. Sides of transverse shelf dark reddish-brown.
Thorax: Mesonotumm reddish-brown; metanotum darker reddish-brown. Pleura reddish-brown with membranes grayish tinged with red. Prothoracic leg reddish-brown, femur lighter brown or yellowish basally, tarsi lighter reddish-brown tinged with red; meso- and metathoracic legs yellowish, apical portion of femur reddish to reddish-brown, tarsi reddish-brown or tinged with red. Wings hyaline with all veins reddish-brown; forewings with costa, subcosta, and often radial spaces tinged with reddish-brown and crossveins heavily

margined with reddish-brown; hindwings broadly tinged with red on outer margins.

Abdomen: Terga 1-10 reddish-brown; terga 1-8(9) with a light reddish or orangish middorsal stripe, stripe bordered laterally by dark brown to black streaks; terga 1-7(8) with narrow brown bands on posterior margins; terga 1-10 with posterolateral angles dark brown (Fig. 26). Pleural fold margined with dark brown. Sterna 1-10 reddish-brown to orangish red; sterna 1-10 with a light reddish midventral stripe, stripe bordered by oblique blackish submedian streaks; sterna 2-6 with 2 pair of transverse black dots; sterna 7(8) with 1 pair of black spots. Caudal filaments whitish to yellowish, basally tinged with red to reddish-brown, articulations sometimes very lightly tinged with red. Forceps dark reddish-brown. Genitalia as Fig. 4 .

Female Imago:

Body: length 17-19 mm, forewings 16-18 mm.

Head: Reddish brown to orangish; ocelli grayish with ocellar elevations blackish tinged with brown; head dorsally with yellowish middorsal stripe; posterior angles of occiput blackish. Antennae brownish red.

Thorax: Mesonotum light reddish-brown; metanotum darker reddish-brown. Pleura reddish-brown, membranes grayish tinged with red. Prothoracic leg reddish-brown, femur yellowish basally, tarsi light reddish-brown. Meso- and metathoracic legs yellowish, apical portion of femur reddish to reddish brown, tarsi tinged with red. Wings hyaline with all veins reddish-brown; forewings with costal and subcostal spaces tinged with reddish-brown, crossveins heavily usually heavily margined with reddish-brown, bullae often tinged with reddish-brown; hindwings broadly tinged with red on outer margins.

Abdomen: Terga 1-10 reddish-brown to orangish-brown; terga 1-9(10) with a light reddish middorsal stripe, stripe bordered laterally by blackish streaks; terga 1-9(10) with narrow brown bands on posterior margins; terga 1-10 with posterolateral angles dark reddish-brown. Sterna 1-10 reddish-brown to orangish; sterna 1-10 with a light midventral stripe, stripe bordered laterally by oblique blackish submedian streaks; sterna 2-5(6) with 2 pair of transverse dots; sterna 6-7(8) with 1 pair of transverse dots. Prominent lateral extensions of segment 9 semitranslucent. Caudal filaments yellowish, basally tinged with red, articulations often very lightly tinged with red. Subanal plate deeply emarginate.

Egg: Typical of subgenus, knob-terminated coiled threads densely covering entire egg (Figs. 55-56).

Nymph:

Body length 17-22 mm.

Head: Nota dark yellowish-brown to dark brown sometimes with a faint coronal whitish stripe. Antennae brown, distal portion flagella light brown to grayish.

Thorax: Nota dark yellowish-brown to dark brown, sometimes with faint whitish middorsal stripe. Pronotum with 2 pairs of faint submedian marks. Legs dark brown with whitish or yellowish markings; forefemora either with a median yellowish or whitish spot or transverse band and a wide apical transverse band, tibia whitish or yellowish with a wide dark brown submedian transverse band, tarsi dark brown yellowish apically; tarsal claws with 7-10 marginal denticles. Procoxal gills a tuft of multibranched whitish filaments.

Abdomen: terga dark yellowish-brown; terga 1-9 with faint yellowish narrow middorsal stripe, often more distinct on anterior portion of terga, stripe bordered by a pair of submedian oblique streaks; terga 1-9 margined with black. Sterna dark yellowish-brown; sterna 1-10 with whitish oblique submedian streaks and 2 pair of whitish transverse dots. Gill lamella light grayish brown, median sclerotized ridge brown, anterior edge of lamella sclerotized; fibrillar portion whitish purple. Caudal filaments dark yellowish-brown, lighter near tip, brownish at apex.

Diagnosis:

Adults of this beautiful species can be easily distinguished from all other species of the genus by any of the following characters: (1) wing maculation, (2) abdominal maculation, (3) large body size, and (4) restricted distribution (California and Oregon).

Mature nymphs are very distinctive and can be distinguished by the following combination of characters: (1) rather uniform yellowish-brown body color, (2) large body size (17-22 mm), and (3) restricted geographical distribution.

Discussion:

Isonychia velma is very unique and distinctive in all stages, apparently not closely related to any other North American species of the *bicolor* group. No very recent adult nor nymphal material was available for study, with most specimens collected in 1930's or late 1940's. Allen and Edmunds (1956) first reported this species from Oregon.

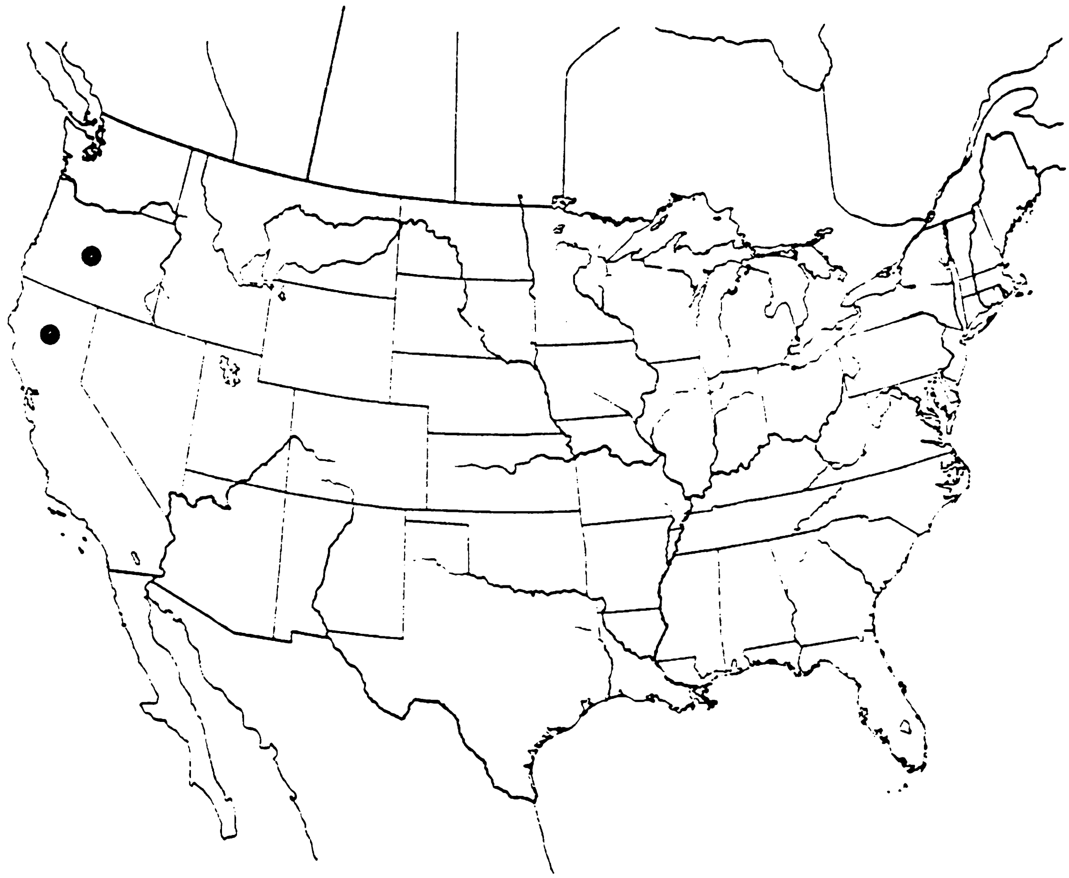
Biology:

Day (1952) reported that this species is widespread in northern California and usually found in larger rivers (e.g. Klamath, Trinity, Russian, and Putah Creek). Nymphs were collected in shallow riffles, many times on wooden substrates. This species is apparently a late emerger with adults collected from August to December.

Material:

Holotype M (parts on 2 slides), California: Putah Creek near Maticello, ? Dec 1917, T. C. Bradley; Paratypes, 2 F (1 F on slides), same as Holotype; 13 F, Cloverdale, 4 Oct 1917, T. C. Bradley.

California: Eel River at Red Mt. Creek, 1 Sept 1950, E. Rishel, 4 N (CAS); Eel River, 1 1/2 mi. S of Oyerville on US 101, 14 Sept 1946, H. G. Nelson, 2 N (INHS); Klamath River, 1 mi W. of Scott River, ? Aug 1949, W. C. Day, 1 M (reared); 45 N (CAS); Manchester, Alder Creek, 7 Sept 1932, P. R. Needham, 1 N (CU); Mendocino Co., Boonville, 12 N (CAS); Monticello, 25 May 1947, H. P. Chandler, 1 N (CAS); Plumas Co., 29 Aug 1946, H. P. Chandler, 1 N (CAS); Putah Creek, Monticello, 1 Oct 1949, W. C. Day, 9 N (CAS); Sonoma Co., Russian River, Geyserville, 15 Oct 1949, W. C. Day, 11 N (CAS), 5 N (CNC), 2 N (UU); Trinity Co., Weaverville, 16 Sept 1946, H. P. Chandler, 2 N (CAS); Trinity River, 30 mi. E of Willow Creek P.O., ? Aug 1949, W. C. Day, 2 F (reared) (CAS); Oregon: Foster, 14 Oct 1934, R. Dimick, 10 F (UU); Foster, Santiam River, 14 Oct 1934, R. E. Dimick, 1 M, 1 F (CNC) Linn Co., Williamson River, Corvallis, 22 Oct. 1937, E. E. Crawford, 1 M, 1 F (UU).



Map 4. Distribution of I. velma Needham.

Arida Group

Male Imago:

Genitalia: Penes with ventral lobes broadly rounded apically; dorsal lobes narrowly rounded apically; each dorsal lobe with a small medial slightly sclerotized flap.

Isonychia (*Isonychia*) *arida* (Say)

Figs. 6, 7, 58, 59

Baetis arida Say, 1839: 42. Type locality: Indiana. Type destroyed.

Isonychia arida, Burks, 1953: 111.

Isonychia pictipes Traver, 1934: 250. Type locality: Williamson Swamp, Bartow, Georgia, M, F. Type deposition (M) CU; Traver 1935: 495; Berner, 1950: 111; Kondratieff and Voshell (In press).

Male Imago:

Body: length 8-14 mm, forewings 8-13 mm.

Head: eyes purplish-gray with dorsal portion separated by lighter transverse bands.; ocelli whitish; ocellar elevations black. A black spot between compound eyes and scape. Antennae brownish.

Thorax: Mesonotum light reddish-yellow to reddish-brown; metanotum dark reddish-brown (Fig. 7). Pleura yellowish, membranes tinged with purplish. Prothoracic leg reddish-brown, femur often darker apically, usually margined with black apically, tibia whitish medially, dark reddish brown at base and tip, tarsi whitish to light brown; meso- and metathoracic legs yellowish, often lightly tinged with brown. Wings hyaline with all veins whitish to yellowish; forewings with stigmatic region stained with whitish.

Abdomen: Terga 1-9 light red to reddish-brown; terga 1-8(9) purplish-black bands on posterior margins; terga 1-9 often with a faint light reddish middorsal stripe bordered by light submedian marks. Sterna light reddish to dark reddish-brown; sterna 1-8(9) with light purplish black bands on posterior margins; sterna 1-9 with gray to grayish-black band paralleling pleural fold. Pleural fold margined with purplish-gray. Caudal filaments whitish to yellowish with dark articulations, basal segments occasional lightly marked with brown. Forceps yellowish. Genitalia as Fig. 6.

Female Imago:

Body: length 11-16.5 mm, forewings 11-16 mm.

Head: Creamy yellow to dark pinkish; ocelli whitish; ocellar elevations blackish. Posterolateral angles of occiput blackish; a blackish bar or spot below comound eyes and scape. Antennae yellowish to brown, flagella tinted with brown.

Thorax: Mesonotum yellowish-brown; metanotum reddish yellow brown. Pleural yellowish, membranes tinged with purple. Legs colored as male. Wings hyaline with all veins whitish to light yellow, crossveins often light brown to margined with very light black; stigmatic region of forewing whitish.

Abdomen: Terga light red to reddish-brown; terga 1-(9) with purplish-black bands on posterior margins; terga 1-9 with a faint light reddish middorsal stripe. Sterna 1-9 light reddish or light reddish-brown; sterna 1-9 with light purplish black bands on posterior margins. Caudal filaments whitish to yellowish without dark articulations. Subanal plate with a moderate to deep immargination.

Eggs: Spherical, chorion smooth, knob-terminated coiled threads spaced uniformily on surface; knob-terminated coiled threads with prominent triangular knobs (Figs. 57-59).

Nymph:

Body: length 7-14 mm.

Head: Brown to light brown with whitish coronal stripe. Antennae whitish, scape and usually pedicel tinged with brown, flagella occasionally lightly tinged with brown.

Thorax: Nota brown to light brown usually with a whitish middorsal stripe; pronotum with 2 pairs of submedian whitish spots or bilobed marks; small whitish to yellowish spots and streaks anterior and lateral of mesothoracic wing pads; mesonotum with a pair of whitish often oblong median spots, spots often fused with middorsal stripe. Legs light brown with whitish markings; forefemora light brown with faint whitish basal, median, and apical spots or transverse bands, tibia whitish to yellowish-brown median brownish transverse band, tarsi whitish with a basal transverse band; tarsal claws with 6-11 marginal denticles.

Procoxal gill a tuft of multibranched purplish filaments.

Abdomen: Terga 1-9 yellowish brown; terga 1-9 with a variable whitish or yellowish middorsal stripe, often faint or absent; lateral margins of terga 1-9 often mottled with white; terga 2-9 often with posterior margins margined with purplish-black; terga 10 whitish or yellowish anteriorly, brownish posteriorly. Sterna yellowish-brown; sterna 1-9 with blackish spot at lateral edge. Gill lamella purplish or with a purplish median spot; median sclerotized ridge brown; fibrillar portion purplish. Caudal filament yellow brown, often darker, each filament with a broad brown transverse band near middle, a broad brownish or blackish transverse band near tip, between these bands, filaments whitish.

Diagnosis:

Adults of this distinctive species may be distinguished by any of the following characters: (1) distinct bicolored foretibia, (2) penes, and (3) interesting eggs.

The nymph was positively associated for the first time and is very similar to the nymphs of the eastern species of the bicolor group. Apparently the only reliable means of separation requires slide mounting forelegs of mature nymphs. The characteristic bicolored pattern of the foretibia is revealed through the nymphal cuticle.

Discussion:

The correct identification of this species was first clarified by Burks (1953) after collecting an Illinois male with "anterior tibiae whitish, obscure at base and tip." The original description by Say (1839) of Indiana specimens was typically brief and, therefore, Walsh (1862) apparently incorrectly identified specimens, now known as *I. sayi* Burks, as *I. arida* (Say). Hagen (1863) noticed that Walsh's specimens had foretibiae completely dark but apparently considered this within the normal range of variation. McDunnough (1931) also doubted Walsh's original identification but did not decide to change the "generally accepted idea of the species." Burks (1953) however, collected a specimen which "fully agreed with

Say's description" and renamed *I. arida* of Walsh, *I. sayi*.

Traver (1934) described *I. pictipes* from male and female imagoes from Williamson Swamp Creek, Bartow (Jefferson County), Georgia and from the Apalachee River, north of Monroe, the Alcova River, south of Monroe (Walton County), Georgia. She distinguished this species from all other *Isonychia* by its bicolored foretibia. It is interesting to note that if Burks keyed his Illinois specimen through Traver (1935), it would have readily keyed to *I. pictipes*.

Kondratieff and Voshell (In press), after examining the Illinois specimen and *I. pictipes* from throughout its range, designated *I. pictipes* as a junior synonym of *I. arida*. Since no type specimen of *I. arida* is known and a synonymy is involved, I designate the Illinois male imago listed by Burks (1953) as a Neotype of *I. arida* (Say) (In INHS Collection).

Biology:

Berner (1950) reported some biological information on this species in Florida. Adults were collected from

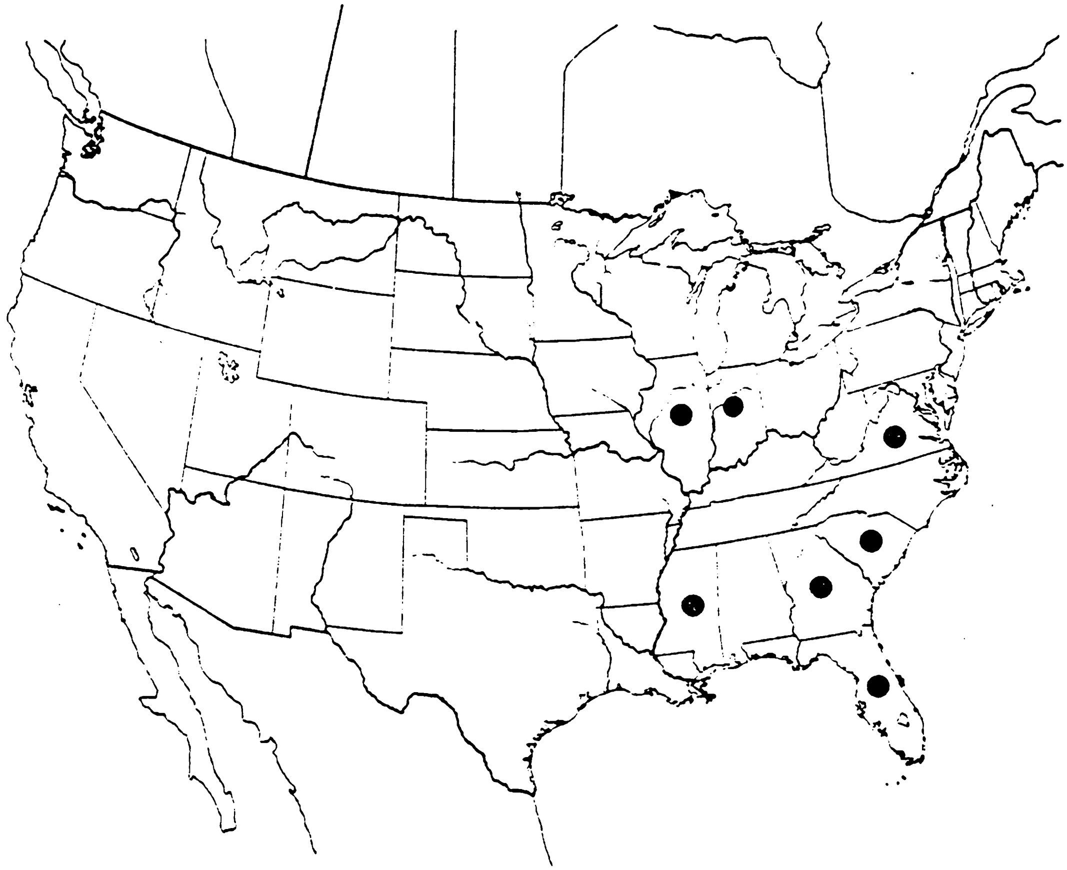
May to July and in December. He stated that the life history was the same as *I.* sp. A (see Biology section under *I. sayi*). Kondratieff and Voshell (In press) reported additional life history information of this species.

Material:

Neotype M, *Isonychia arida*, Illinois: Momence, 16 Aug 1936, H. H. Ross and B. D. Burks (INHS). Holotype M, *Isonychia pictipes*, Georgia: Williamson Swamp Creek, Bartow, 31 May 1931, P. W. Fattig (CU# 1257.1); Allotype F, Apalachee River N of Monroe, 12 Aug 1931, P. W. Fattig (CU# 1257.2); Paratypes, 6 M, same as Allotype (4 M, CU# 1257, 2 M, CU); 2 M Alcova River S of Monroe, P. W. Fattig (CU).

Florida: Calhoun Co., Chipola River at Hwy. 20, 14 April 1972, P. H. Carlson, 3 M, 5 F (FAMU); same but 20 April 1972, 5 M, 5 F (FAMU); same but 15 June 1972, 4 M, 5 F (FAMU); same but 8 July 1972, 4 M, 2 F (FAMU); Dixie, Levy, Gilchrist Cos., Suwannee River at Hwy. Alt. 27, 9 May 1975, P. H. Carlson, 3 M (FAMU); Gadsden Co., Rocky Comfort Creek at bridge, 6 mi. SW of

Hwy. 268 on Hwy. 65 C, 5 May 1973, P. H. Carlson, 2 M (FAMU); Rocky Comfort Creek on dirt rd at bridge 6 mi. S St. Hwy. 268, 10 April 1974, J. Jones et al., 4 M (FAMU); same but 30 April 1974, 4 M, 2 F (FAMU); Jackson Co., Rocky Comfort Creek at Hwy. 71 ,at light, 2 Nov 1975, R. D. Kaplan et al., 3 M, 4 F (FAMU); Rocky Comfort Creek at bridge on dirt Rd., 6 mi. S of St. Hwy. 268, 9 Aug 1967, G. C. Cooper and J. Jones, 43 N (FAMU); Leon Co., Ochlockonee River River, Ochlockonee Wildlife Mgmt. Area, downstream from Tower Rd., N of Tallahassee, 14 Sept 1980, H. M. Savage et al., 5 N (VPI); same but 18 Oct 1980, 3 F (FAMU); same but 23 April 1981, 2 M, 1 F, 3 N (FAMU); same 1 M, 2 sub M, 4 F (VPI); Liberty Co., Apalachicola River at Hwy. 20, Bristol, 15 July 1973, P. H. Carlson, 1 sub M (FAMU); Rock Creek, 4 June 1953, LB, 1 N (UF); Okaloosa Co., Yellow River on Hwy. 2, 1/2 mi. E of Oak Grove, 25 April 1967, W. L. Peters et al., 2 M, 3 F (FAMU); Walton Co., Choctawhatchee River at Hwy. 20 (W side of river), 14 Aug 1971, P. H. Carlson, 3 F (FAMU); Washington Co., Choctawhatchee River, 1 1/2 mi. W of Live Oak at boat landing, W of Hwy. 284, 1 Oct 1971, P. H. Carlson, 1 M (FAMU); Georgia: Baker Co., Chickasawhatchee River at Hwy. 37, ca 10 mi. W of Newton, 11 Sept 1971, P. H. Carlson, 1 M, 1 F (FAMU); Cherokee Co., Etowah River at Junction of St. Rd. S 861, 6 1/2 mi. ESE of Ball Ground, 22-25 June 1971, LB et al., 2 F (FAMU); Cherokee Co., LB, 6 M, 1 F (UF); Monroe, Apalachee River, 9 mi E, 29 June 1945, P. W. Fattig, 1 M, 3 F (INHS); Mississippi: Pike Co., Tangipuhoa River, Hwy. 51, 10 June 1977, B. Stark et al., 2 M (FAMU); Walthall Co., Bogue Chitto River, 5 mi. SE of Lexie, 17 June 1977, B. Stark, 4 M, 1 F (FAMU); South Carolina: Aiken Co., Upper Three Runs Creek, about 0.1-1.0 mi. upstream drom SRP Rd. C and about 8 mi. S of New Ellenton, 7 June 1972, J. W. Richardson, 2 M, 2 F (ANSP); same but below bridge at Hwy. A, 25-26 Aug 1964, J. D. Gentry, 2 F (ANSP); Virginia: Louisa Co., South Anna River, St. Rt. 522, 5 July 1977, BCK, 2 M 2 F (VPI); same but 19 July 1977, 6 M, 2 F (VPI).



Map 5. Distribution of I. arida (Say).

Sicca Group

Male Imago:

Genitalia: Penes with ventral lobes broadly rounded, subtruncate or narrowly rounded apically; dorsal lobe without prominent flap, at most a slightly sclerotized medial margin (Figs. 8-12).

Key to Male Imagoes

of the *Sicca* Group

1. Abdominal terga purplish red-brown with large yellowish to whitish anterolateral triangular spots (Fig. 28) - - - - *intermedia* (Eaton)

   Abdominal terga not purplish red-brown and lacking pale anterolateral spots - 2

2. Abdominal terga light yellowish-brown; abdominal terga 1-10 with a pair of submedian dorsal oblique to parallel purplish-brown streaks (Fig. 27); forewings with brownish spots or bars in second and third bulla interspace (Fig. 33); distribution Mexico south to Honduras (Map 8) - *edmundsi* n. sp.

   Abdominal terga not exactly as above; forewings without brownish spots or bars in second and third bulla interspace; distribution Mexico north to Alberta and Florida (Maps 6, 7, 9, and 10) - - - - 3

3. Penial lobes narrowly rounded distally (Fig. 8) - *berneri* n. sp.

   Penial lobes broadly rounded to subtruncate distally (Figs. 9 and 12) - 4

4. Abdominal terga 1-9 dark reddish-brown to reddish-orange without distinctly darker lateral shading of terga; distribution as Map 10 - *sicca* (Walsh)

   Abdominal terga 1-9 light brownish, distinctly shaded laterally with darker brown; distribution as Map 7 - - - *campestris* McDunnough

Isonychia (Isonychia) berneri

new species

Figs. 8, 60, 61

Body: length 9-12 mm, forewings 9-11 mm.

Head: Eyes purplish-gray with dorsal portion separated by darker and lighter transverse bands; ocelli grayish; ocelli elevations purplish-black. A black streak between compound eye and scape. Antennae whitish, tinged with brown.

Thorax: Meso- and metanota yellowish-brown, shaded with dark brown; Pleura yellowish-brown, membranes purplish. Prothoracic leg reddish-brown, femur lighter brown basally, tarsi whitish, often tinged with light brown; meso- and metathoracic legs yellowish, claws often lightly tinged with purple. Wings hyaline with all veins whitish to very light brown; forewing with stigmatic region stain with white, few crossveins anatomosed.

Abdomen: Terga dark reddish-brown; terga 1-9 with posterolateral margins purplish-black bands; terga 1-9 with a faint reddish-brown middorsal stripe, stripe bordered by submedian oblique light reddish-brown streaks; terga 1-9 with a anterolateral purplish-black mark; terga 1-9 wih lateral margins margined with purplish-black; terga 10 yellowish sometimes tinged with brown. Sterna reddish-brown usually darker than dorsum; sterna 1-9 with posterolateral margins light purplish-black bands; sterna 1-9 with a pair of dark purplish brown or light reddish-brown submedian oblique streaks and often a pair of reddish-brown spots. Caudal filaments whitish. Forceps yellowish tinged with reddish-brown. Genitalia as Fig. 8.

Female Imago:

Body: length 10-13 mm, forewings 10-12 mm.
Head: Yellowish; ocelli grayish; ocellar elevations purplish-black; dorsally with a pair of brownish stripes. Posterolateral angles of occiput black; a blackish spot or dash below compound eye and scape. Antennae whitish, tinged with brown.
Thorax: Meso- and metanota yellowish-brown, mesoscutellum and metanotum shaded with darker brown. Pleura yellowish-brown, membranes purplish. Prothoracic leg reddish-brown, lighter basally, tarsi whitish, articulations often tinged with reddish; meso-

and metathoracic legs yellowish, claws tinged with purple. Wings hyaline with all veins whitish to very light brown; stigmatic region of forewing stained with white.

Abdomen: Terga reddish-brown; terga 1-9 with posterolateral margins purplish black bands; terga 1-9 with faint reddish-brown middorsal stripe, stripe bordered by submedian oblique light reddish streaks; terga 1-9 with a anterolateral purplish-black to brown mark, sometimes faint; terga 1-9 with lateral margins margined with purplish-black; tergum 10 yellowish often tinged with brown. Sterna reddish-brown often with a purplish tint; sterna 1-9 with posterolateral margins light purplish-black bands; sterna 1-9 usually with a pair of light reddish or sometimes dark purplish brown submedian oblique streaks. Caudal filaments whitish. Subanal plate with a moderate emargination.

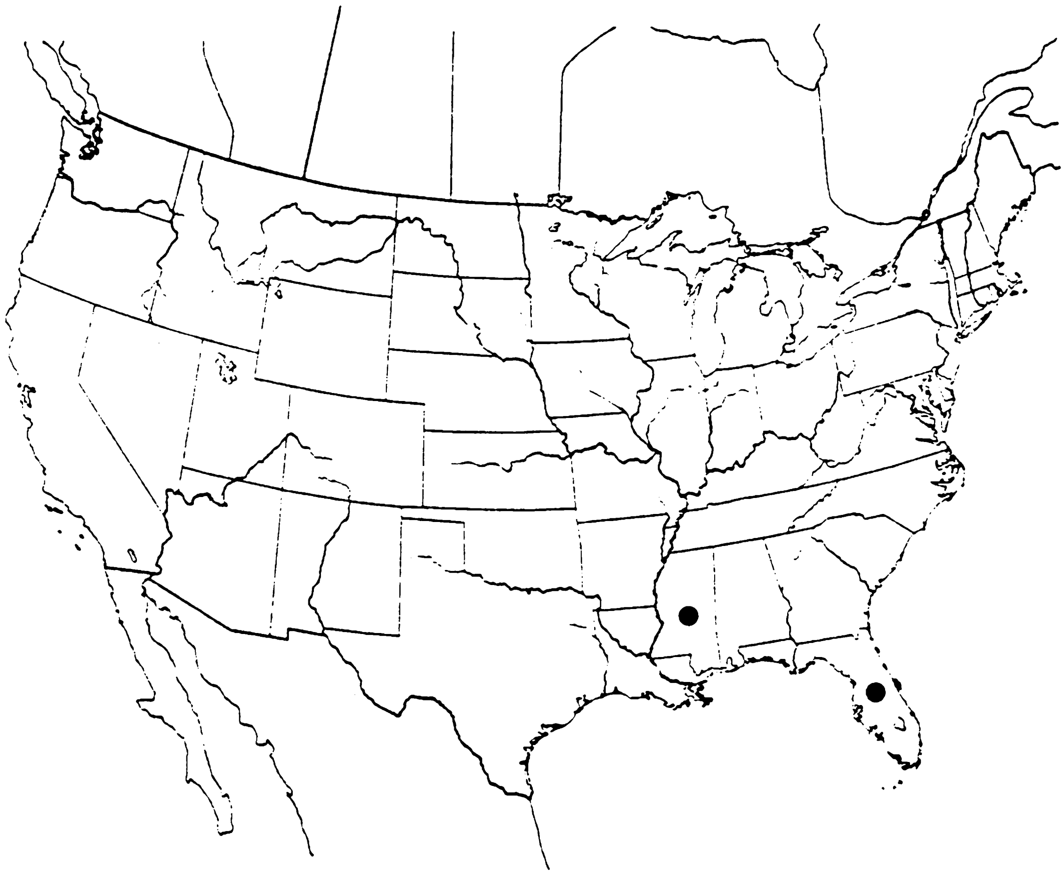
Egg: Somewhat atypical; knob-terminated coiled threads scattered over most of the chorion, larger coïled threads at one pole (Figs. 60-61).

Nymph: unknown

Material:

Holotype M, Florida: Santa Rosa County, Blackwater River at Deaton Bridge, 3.5 miles North of Harold, 10 July 1967, W. L. Peters et al.

Paratypes: Same as holotype, 2 M; Okaloosa County, Blackwater River, Florida A & M University Biological Station, 4.5 miles northwest of Holt, 15 April 1977, W. L. Peters et al., 2 M, 2 F; same but 28 July 1973, 10 M, 6 F; same but 15 July 1976, 10 M; same but 4.5 miles northwest of Cannon Town, 26 April 1967, 3 M; Okaloosa County, Blackwater River, 23 April 1976, L. Berner (Cat. No. 4-2376-1, no. 4480.0), 1 M; Mississippi: Claiborne County, Little Sand Creek, Rocky Springs, NTP, 28 April 1978, B. P. Stark, 1 M; Simpson County, Mill Creek, Hwy 472, 4 mi SE of Pinola, 16 Oct 1981, B. P. Stark, M. Britton, 1 M.



Map 6. Distribution of I. berneri n. sp.

The holotype and the majority of the paratypes are deposited in the Florida A & M University Collection. Additional paratypes are deposited in the Florida State Collection of Arthropods, Gainesville and VPI&SU collection.

Etymology:

This species is named in honor of Dr. Lewis Berner, University of Florida, for his numerous contributions to the study of Nearctic mayflies.

Diagnosis:

This species is easily distinguished from others of the subgenus Isonychia by the following combination of characters: (1) penial lobes narrowly rounded distally, (2) wings hyaline, venation whitish to very light brown, and (3) terga 1-9 with prominent anterolateral purplish-blacks marks.

The nymph is presently unassociated. Nymphs probably of this species were examined from the Blackwater River, Florida and from Mississippi. However, rearing is required for a positive association.

Discussion:

The male imago of this species is very distinctive and cannot be confused with any other species of Nearctic *Isonychia* s.s. The shape of the penes is unusual for this group. Some variation was noted in the penial form. Occasionally some individuals had additional thin membranous tissue between the penial lobes giving the penes a broader appearance medially.

This species is presently known only from Florida and Mississippi, and has been previously been identified as *I. fattigi* Traver, a synonym of *I. bicolor* (Berner 1977). It is interesting to note the high diversity of unusual or apparently endemic mayfly species of the Blackwater River (Peter and Jones 1973, Berner 1978).

Biology:

This species is apparently common in the Blackwater River, a shifting sand river in northwestern Florida. Water quality data for this river has been summarized under *I. sayi*. Adults examined were collected from April to July.

Isonychia (*Isonychia*) *campestris*

McDunnough

Figs. 9, 62, 63

Isonychia sicca campestris McDunnough, 1931: 161. Type locality: Medicine Hat, Alberta, Canada, M, F. Type deposition: (M) CNC.

Isonychia campestris, Traver, 1935: 487.

Male Imago:

Body: length 9-14 mm, forewings 9-13 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter transverse bands; ocelli whitish to grayish; ocellar elevations black. A blackish streak between compound eye and scape. Margins of transverse shelf and keel usually margined with black. Antennae whitish tinged brown.

Thorax: Meso- and metanotum light brown to yellowish-brown; mesoscutellum and metanotum dark reddish-brown. Pleura yellowish, membranes tinged with purplish. Prothoracic leg reddish-brown to dark reddish-brown, femur often lighter basally, tarsi light brown to reddish. Meso- and metathoracic leg whitish to yellowish, sometimes tinged with red. Wings hyaline with all veins brownish to blackish; stigmatic region of forewing stained with white, few to numerous crossveins anatomosed.

Abdomen: Terga 1-9 light brown with posterolateral margins purplish-black, often reduced laterally; terga 1-9 shaded laterally with dark brown to reddish-brown, often diffusely; terga 1-7(8) usually with a pair of submedian light oblique streaks; terga 7-9 often lighter brown. Sterna 1-10 light brown. Caudal filaments whitish to light yellowish-brown with at least 1-4 or more articulations brownish, basally segments also often lightly shaded with brown. Forceps light brown. Genitalia as Fig. 9.

Female Imago:

Body: length 10-15 mm, forewings 10-14 mm.

Head: Yellowish to light brown; ocelli whitish or grayish; ocellar elevations blackish. A brownish or blackish streak or blotch laterally between compound eye and ocelli; dorsally often with a pair of reddish-brown stripes. Median carina of transverse shelf often often margined with dark brown. Antennae whitish often tinged with brown.

Thorax: Meso- and metanotum yellowish to yellowish-brown tinged with brown. Pleura yellowish, membranes tinged with brown. Prothoracic leg reddish-brown, femur lighter basally, tarsi light brown to reddish; meso- and metathoracic legs whitish or yellowish, sometimes tinged lightly with reddish. Wings hyaline with all veins brownish to blackish, crossveins often darker; stigmatic region of forewing stained with white, crossveins usually anastomosed.
Abdomen: Terga 1-10 light brown; terga 1-9 with posterolateral margins purplish black, often reduced to transverse dashes; terga 1-9 shaded laterally with brown, often more pronounced on anterior terga. Sterna 1-10 light brown to yellowish-brown. Caudal filaments whitish to yellowish with no distinctly darker articulations, often lightly shaded basally with brown. Subanal plate moderately to deeply emarginate.
Egg: Typical for subgenus; knob-terminated coiled treads densely packed on 1 hemisphere and scattered on the other (Figs. 62-63).

Nymph:

Body length 10-15 mm.

Head: Light reddish-brown to yellowish-brown with a whitish or yellowish coronal stripe, often mottled dorsally. Antennae whitish, often tinged with very light brown.

Thorax: Nota reddish-brown to yellowish-brown with a middorsal whitish or yellowish stripe; pronotum with 2 pairs of submedian crescentric or bilobed whitish or yellowish spots; mesonotum with whitish or yelllowish spots anterior and lateral of wing pads; mesonotum often with 2 submedian whitish spots. Legs reddish-brown to brown with yellowish marks; forefemora yellowish with subbasal and subapical reddish-brown transverse bands, often entirely mottled with reddish-brown, tibia yellowish-brown to whitish with a wide reddish-brown transverse band, tarsi yellowish with a wide median brown transverse band; tarsal claws with 7-11 marginal denticles. Procoxal gills in tufts of multibranched purplish or whitish filaments.

Abdomen: Terga yellowish to reddish-brown; terga 1-9 usually with a yellowish or whitish middorsal stripe; terga 1-9 with a whitish spot near lateral margin; terga 10 reddish-brown posterolaterally, yellowish anteriorly. Sterna yellowish-brown to reddish-brown;

sterna 2-6 usually with 2 pairs of whitish midventral transverse dots, sterna 7-9 with a pair of whitish midventral dots; sterna 1-9 often with a pair of submedian whitish streaks. Gill lamella light purplish to whitish, median sclerotized ridge usually brown; fibrillar portion light purplish. Caudal filaments yellowish to reddish-brown, usually darker basally, each filament with a submedian brownish wide transverse band, posterolateral of this band filaments often yellowish to whitish, extreme tips sometimes tinged with black or brown.

Diagnosis:

Isonychia campestris may be distinguished by the following combination of characters: (1) terga 1-9 light brown, distinctly shaded with darker brown laterally, and (2) distribution- Alberta east to Manitoba south to Utah. The nymph is very similar to *I. sicca* and *I. edmundsi* and can be presently only identified by its distribution.

Discussion:

This species was described as a "variety" of *I. sicca* by McDunnough (1931) from specimens collected in southern Alberta. He also noted specimens from Saskatchewan and Manitoba. Traver (1935) considered it as a valid species. *Isonychia campestris* is also considered here as a valid geographically restricted species. It is relatively consistent with little variation noted other than size. Further study and collecting may indicate that there is character overlap and lack of reproductive isolation with *I. sicca*. *Isonychia campestris* probably arose from an *I. sicca* population north and west of the present range of the latter species. Edmunds (1954) first listed *I. campestris* from Utah.

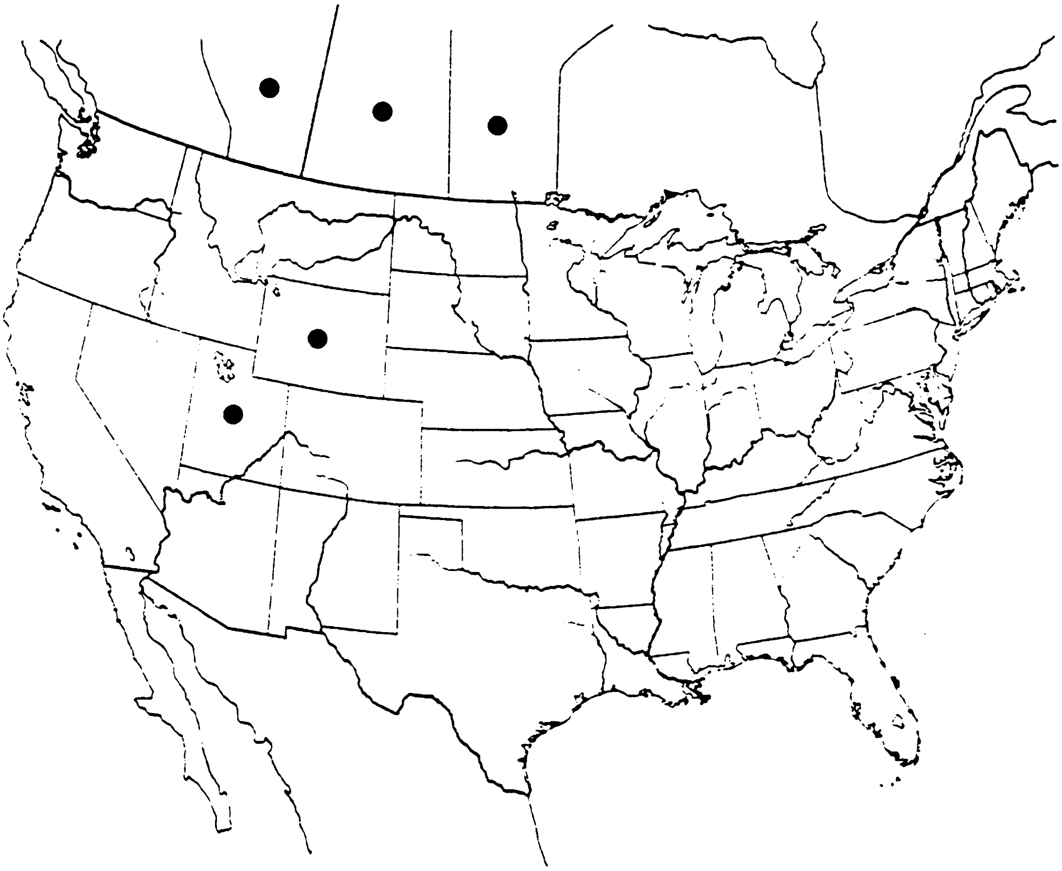
Biology: Little information is available. Adults have been collected from July to September.

Material:

Holotype M, Canada: Alberta, Persons Creek, Medicine Hat, 6 August 1929, J. H. Pepper (CNC# 3252), male genitalia slide only; Paratypes, same as Holotype, 1 M (CNC); Medicine Hat, 24 July 1930, 1 F (INHS); Medicine

Hat, Sask. River, 9 Aug 1929, J. H. Pepper, 1 F (CNC); Milk River, 23 Aug 1929 (CNC), male genitalia slide only.

Canada- Alberta, Lethbridge, 29 July 1930, J. H. Pepper, 2 F (AMNH); Medicine Hat, 21-26 Aug 1929, F. S. Carr, 2 M (AMNH); Milk River, 23 Aug 1929, J. H. Pepper, 1 F (AMNH); Battle Creek, 20 April 1975, R. S. Demaray, 4 N (RD); Milk River, Hwy. 878, 22 July 1980, D. A. Soluk, 67 N (DAS); Red Deer River near Dinosaur Prov. Park, Hwy. 876, 16 Oct 1981, D. A. Soluk, 2 N (DAS); Sand River at mouth, 50 23'N 111 2'W, 3 July 1977, L. J. D. A. Soluk, 1 M, 1 sub M, 4 F (reared), 29 N (DAS); same but 9 July 1978, 3 M, 1 F (DAS); Saskatchewan, North Saskatchewan River, Borden, Hwy 5, 20 July 1974, R. S. Demaray, 12 N (RD); same but 27 July 1974, 1 F (reared) (RD); same but 24 July 1975, 1 M, 1 F (reared) (RD); South Saskatchewan River, Lemsford Ferry, 18 July 1975, R. S. Demaray, 8N (RD); South Saskatchewan River Leader, 31 Aug 1975, R. S. Demaray, 5 F (reared) (RD); same but Hwy. 32, 5 Sept 1975, 1 M, 1 F (reared) (VPI); United States- Wyoming: Tarington, 17 July 1947, D. G. Denning and R. E. Pfadt, 4 M, 1 F (INHS); Wheatland, 29 Aug 1967, R. E. Pfadt, 7 M, 4 F (UU); Sweetwater Co., Green River, 16 July 1959, C. Smith and Musser, 8 N (UU); same but Black's Fork River at Int. Hwy. 80, 6 mi. E of Little America, 21 July 1971, S. L. Jensen and A. V. Provonsha, 39 M, 2 F (UU).



Map 7. Distribution of I. campestris McDunnough.

Isonychia (Isonychia) edmundsi

new species

Figs. 10, 27, 33, 64, 65

Isonychia sicca manca, Allen and Cohen, 1977: 399. In part.

Male Imago:

Body: length 14-16 mm, forewings 15-15 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter and darker transverse bands; ocelli grayish, ocellar elevations blackish. A purplish black spot or dash between compound eye and scape. Antennae light brown, lightly tinged with purple. Sides of transverse shelf tinged with purple; median ridge and lateral ridge of transverse shelf margined with purple.

Thorax: Prothorax purplish brown usually with a pair of oblique blackish streaks, anterior and laterial margins purplish; mesonotum yellowish-brown to reddish-brown, scutellum tinged with brown and purple; metanotum yellowish brown tinged with darker brown. Pleural yellowish-brown, membranes whitish to yellowish with some purple tinting. Prothoracic leg yellowish-brown, tinged with reddish-brown; meso- and metathoracic legs yellowish. Wings hyaline with all veins reddish to dark margined; second and third bulla interspace of forewing with a brown spots (Fig. 33), stigmatic region stained with brown, few crossveins anatomosed.

Abdomen: Terga light yellowish-brown, terga 1-9 with wide purplish bands on posterolateral margins; terga 1-10 with a pair of submedian oblique to parallel purplish brown streaks; terga 2-9 with brownish anterolateral streak (Fig. 27). Sterna yellowish-brown; sterna 1-9 with reddish purple bands on posterolateral margins; sterna 2-5(6) with a pair of submedian oblique streaks and 2 pairs of brownish transverse dots; sterna 5-9 with a pair of submedian oblique streaks and transverse brownish dots. Caudal filaments yellowish to light brown, basal segments lightly shaded with yellowish-brown. Forceps yellowish. Genitalia as Fig. 10.

Female Imago:

Body: length 16-18 mm, forewings 15-17 mm.

Head: Yellowish to very light brown; ocelli grayish, ocellar elevations blackish. A purplish-black spot or streak between compound eye and lateral ocelli; a blackish streak between compound eye and scape; head dorsally with a pair of brownish purple stripes. Antennae light brown tinged with purple; sides of transverse shelf tinged and margined with purple. Thorax: Prothorax purplish brown; mesomotum and metanotum yellowish-brown tinged with purplish brown. Pleura yellowish-brown, membranes yellowish tinged with purple. Prothoracic leg yellowish-brown, femur often darker apically; meso- and metathoracic legs yellowish, tarsi and claws inged with purplish red. Wings hyaline with all veins reddish-brown to dark brown; third bulla interspace of forewing with a brown spot, stigmatic region stained with whitish to light brown (Fig. 33). Abdomen: Terga light yellowish-brown; terga 1-9 with wide purplish bands on posterolateral margins; terga 1-10 with a pair of oblique to parallel brownish streaks, often faint on terga 1-6; terga 2-9 with lateral margins brownish. Sterna yellowish, sterna 1-9 with purplish bands on posterolateral margins; sterna 2-9(10) with a pair of submedian oblique often faint streaks. Caudal filaments yellowish to light brown, basal segmemnts lightly shaded with yellow brown. Subanal plate moderately and broadly emarginate.

Egg: Typical of subgenus, knob-terminated coiled threads densely packed on one hemisphere, scattered on the other (Fig. 64-65).

Nymph:

Body: length 15-18 mm.

Head: Light reddish-brown to red brown, with a whitish to yellowish coronal stripe often mottled with brown dorsally. Antennae whitish, scape brownish, flagella tinged with brown.

Thorax: Nota reddish-brown with a whitish or yellowish middorsal stripe; pronotum with 2 pairs of submedian crescentric or curved whitish or yellowish spots; mesonotum with whitish spots and straks anterior and lateral of wing pads; mesonotum with a pair of median whitish spots often fused with middorsal stripe, also with a pair of submedian whitish spots. Legs yellowish with reddish-brown marks; forefemora yellowish with subbasal and subapical reddish-brown transverse bands, tibia whitish yellow with a median brownish transverse band, tarsi·yellowish with a wide median transverse band; tarsal claws with 7-11 marginal denticles. Procoxal gills in tufts of multibranched light purplish filaments.

Abdomen: Terga yellowish-brown to reddish-brown; terga 1-9 with a yellowish to light yellowish-brown middorsal stripe, usually bordered by dark reddish brown; terga 1-9 with small whitish submedian spots or streaks with dark reddish-brown pigment; terga 1-9 with a whitish to yellowish median spot near lateral margin; terga 10 reddish-brown posterolaterally, yellowish anteriorly. Sterna yellowish-brown; sterna 1-9 with anterolateral brownish spot; sterna 1-9 with whitish midventral blotch surrounded by darker brown; sterna 2-6 with 2 pairs of whitish midventral transverse dots; sterna 7-9 with 2 whitish midventral transverse dots. Gill lamella light purplish; median sclerotized ridge; anterior and posterolateral margins brown; fibrillar portion light purplish. Caudal filaments reddish-brown to yellowish, darker brown basally, each filament with a broad darker brown submedian band, posterolateral of this band filaments yellowish to whitish, extreme tip tinged with brown.

Material:

Holotype M, Honduras: Chumloagus, 24 June 1964, J. M. Maltz; allotype F, Honduras: Dept. of Comayagua, Rancho

Chiquito, km 62, 29 May 1964, Blanton, Broce and Woodruff.

Paratypes: 1 F, Honduras: Dept. El Paraiso, Rio Yeguare, Escula Agricola Panamericana, 26 Oct 1964, J. S. Packer; 1 M, same as allotype; 1 M, Mexico: Veracruz, 3 km N of El Fortin, Tenndido River, 1 July 1955, R. B. and J. M. Selander; 1 F, Costa Rica: Prov. of Limon, Los Diamantes Experiment Station, near Guapiles, 18 Sept 1964, R. E. Woodruff.

Map 8. Distribution of *I. edmundsi* n. sp.

The holotype, allotype and all paratypes except the male from Mexico are deposited in the Florida A & M Collection. The male from Mexico belongs to the University of Utah collection.

Etymology:

This species is named in the honor of Dr. George F. Edmunds, Jr., University of Utah for his substantial contributions to the taxomony and phylogeny of mayflies. He recognized this species as new many years ago.

Diagnosis:

Imagoes of I. edmundsi can be distinguished from other species of the sicca group by the following combination of characters: (1) terga 1-9 light yellowish with a pair of submedian oblique to parallel purplish brown streaks, and (2) forewings with brownish spots or bars in second and third bulla interspace.

Nymphs were assigned to this species on the basis of geographic proximity. Allen and Cohen (1977) apparently listed this species in part as records of I.

sicca manca from Honduras. Their northeastern Mexican records were not available for study but most likely do represent *I. sicca*.

Nymphs are very similar to *I. sicca* or *I. campestris*, and cannot be separated other than by geography- Veracruz south to Honduras.

Discussion:

Packer (1965) recognized this species as new in his unpublished thesis on the mayflies of Honduras.

Biology:

Most of the adults were collected from mountainous west central Honduras (elevation ca 300-700 m). Adults from Honduras were collected from May to October; Mexico in July and Costa Rica in September. Packer (1965) found nymphs in water from 1 to 3 feet deep, and in very swift currents.

Material: (Other than types):

Honduras: Dept. Francisco Morazan, 10 miles E of Guaimaca on Highway 3, 6 Nov 1964, J. S. Packer, 1 N (UU); Dept. El Paraiso, Rio Yeguare, Escula Agricola

Panamericana, 26 Oct 1964, J. S. Packer, 1 N (UU); Dept. Comayagua, Rancho Chiquito, km 62, Banton, et al., 1 M subimago (FAMU).

Isonychia (Isonychia) intermedia

(Eaton)

Figs. 11, 28, 38, 39, 66-69

Chirotonetes intermedius Eaton, 1885: 207. Type locality: Arizona, M. Type deposition: (M) British Museum.

Isonychia intermedia, Traver, 1935, 491; Spieth, 1941: 93.

Male Imago:

Body: length 18-20 mm, forewings 18-19 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter and darker transverse bands; ocelli grayish; ocellar elevations brownish black. A purplish spot between compound eye and scape. Antennae light brown. Sides of transverse shelf tinged with purple, median and lateral ridge margined with purple.

Thorax: Prothorax purplish-brown; mesonotum dark yellowish-brown to dark reddish-brown, scutellum dark brown; metanotum dark purplish-brown. Pleura reddish-brown, membranes purplish. Prothoracic leg dark reddish-brown, femur lighter brown, tarsi light reddish-brown to yellowish-red; meso- and metathoracic legs yellowish, often tinged with light red. Wings hyaline with all veins dark reddish-brown to dark brown, venation often lighter basally.

Abdomen: Terga purplish-red-brown; terga 1-9 with darker purplish bands on posterolateral margins; terga 2-9 with large yellowish to whitish anterolateral triangular spots (Fig.); terga 2-9 with yellowish middorsal longitudinal dashes; dashes bordered by brownish red triangular blotches, on terga 6-10 blotches streak-like. Sterna whitish yellow; sterna 2-8(9) with midventral reddish triangles; sterna 2-5(6) with 2 pairs of reddish transverse dots; sterna 6-9 with a pair of darker red streaks. Pleural fold margined with purple. Caudal filaments yellowish with basal segments marked with reddish articulations, basal segments also tinged with red. Forceps yellowish often tinged with red. Genitalia as Fig. .

Female Imago:

Body length 19-22 mm, forewings 19-21 mm.

Head: Yellowish to light brown; ocelli gray; ocellar elevations blackish. A purplish black spot between compound eye and lateral ocelli; a blackish streak between compound eye and scape. Antennae light brown, tinged with purplish. Sides of transverse shelf tinged and margined with purple.

Thorax: Prothorax purplish-brown, margined laterally with purple; mesonotum light yellow brown to reddish-brown; metanotum purplish-brown. Pleura reddish brown, membranes purplish. Prothoracic leg dark reddish-brown, femur lighter brown, tarsi light reddish-brown; meso- and metathoracic leg yellowish often tinged with red. Wings hyaline with all veins dark reddish-brown to dark brown, venation often lighter basally.

Abdomen: Terga purplish to reddish-purplish; terga 1-9 with narrow purplish red bands on posterolateral margins, also yellowish bands anterior to these bands; terga 2-9 with large yellowish white anterolateral triangular spots; terga 2-9 with yellowish white middorsal longitudinal dashes, dashes bordered laterally by brownish red triangular blotches, on terga 5(6)-10 blotches streak-like; terga 9 often diffusely brown. Sterna yellowish white; sterna 1 purplish; sterna 2-6(7) with midventral reddish triangles; sterna 2-7(8) with faint whitish midventral stripe; sterna 2-5 with 2 pairs of light transverse dots. Caudal filament

yellowish white, some basal articulations red, also basally shaded with red. Subanal plate deeply emarginate.
Egg: Typical of subgenus; knob-terminated coiled threads densely packed on 1 hemisphere and scattered on the other (Figs. 66-67).

Nymph:

Body: length: 16-21 mm.
Head: Light reddish-brown to red-brown with a whitish to yellowish coronal stripe. Antennae whitish to yellowish, scape and pedicel often tinged with reddish-brown, flagella tinged with light brown.
Thorax: Nota yellowish to reddish-brown; with a whitish or yellowish middorsal stripe; pronotum with 2 pairs of submedian crescentric or curved whitish or yellowish spots; mesonotum variable, ranging from only with a middorsal stripe and posteromedian oblong spots to a pattern as Fig. 38. Legs yellowish to whitish with reddish-brown marks, forefemora yellowish with reddish-brown subapical transverse band, occasionally femora diffusely brown, tibia whitish with a median reddish-brown transverse band, occasionally tibia light

reddish-brown, tarsi yellowish with a subbasal brownish transverse band; tarsal claws with 10-14 marginal denticles. Procoxal gills in tufts of multibranched light purplish filaments.

Abdomen: Terga 1-9 yellowish-brown to reddish-brown; terga 1-9 usually with a yellowish middorsal stripe, bordered by dark reddish-brown; terga 1-9 often with margins posterolaterally dark reddish; terga 1-9 with small whitish submedian spots or streaks, terga 1-8(9) with a whitish or yellowish median spot near lateral margin; terga 10 reddish-brown posterolaterally, yellowish anteriorly. Sterna yellowish to reddish-brown; sterna 1-9 with anterolateral brownish spot and streak; sterna 1-9 often with lighter midventral blotch and usually two submedian whitish spots; sterna 1-9 often with a pair of submedian crescentric whitish streaks and 2-4 whitish spots; sterna 6-10 often with posterolateral 2/3 reddish-brown. Gill lamella light purplish to whitish; median sclerotized ridge and anterior and posterolateral margins brown; fibrillar portion light purplish. Caudal filaments yellowish-brown to light reddish brown, darker brown basally, each filament with a broad dark brown submedian band, posterolateral of this band filaments whitish, often blackish at extreme tips.

Diagnosis:

Imagoes of I. intermedia are easily distinguished from all other North American Isonychia by (1): terga purplish reddish-brown with large yellowish to whitish anterolateral triangular spots, (2) wings hyaline with all veins dark reddish-brown to dark brown, and (3) large size, 18-22 mm body length.

The nymphs are usually large and conspicuously marked and have numerous stout spines on the leading dorsoapical edge of the prothoracic femur (Fig. 39), separating them from the sicca complex (campestris, edmundsi, and sicca).

Discussion:

This species was described by Eaton (1885) and since then few imagoes have been available for study. The holotype male was not examined. The distinctive abdominal pattern as described by Eaton (1885) and Spieth (1941) left no doubt concerning the correctness of the identification of this species. This species apparently is not as closely related to I. sicca as are the other species in this group.

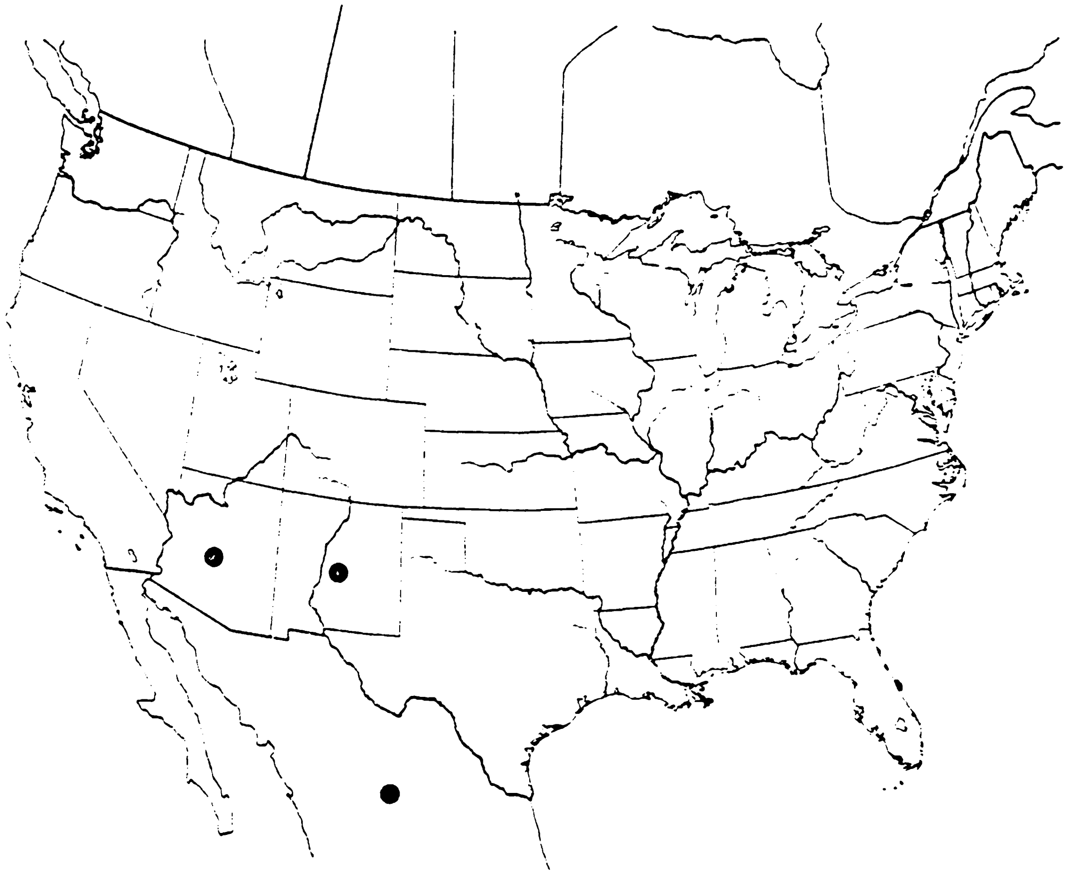
Nymphs of this species have been collected quite commonly by Dr. R. K. Allen in New Mexico and Arizona suggesting it is common in certain streams of the southwest.

Biology:

Little is known about this species. Dr. R. K. Allen has collected numerous mature nymphs in the East Verde, Verde River, and Oak Creek in Arizona. Most mature nymphs examined were collected in mid-July. Mature nymphs were collected in water with temperatures as high as 35°C. Spieth (1950), reporting on the David Rockefeller Mexican Expedition of the American Museum of Natural History to the central plateau of Mexico, noted the similarity of streams of that area of Mexico with streams of southwestern United States. He found I. intermedia common in these streams. He remarked about the ability of adults of I. intermedia to resist disiccation. He found them sitting on bare Acacia twigs in the bright midday sunshine (July 6).

Material:

Arizona: Gila Co., East Verde River on Rd. 406, 10 mi. E of Payson, 19 July 1970, R. K. Allen, 20 N (CAS); Greenlee Co., San Francisco River at Clifton, 95 F, 4 July 1964, R. K. Allen, 1 N (CAS); Yavapai Co., Verde River at Camp Verde, 18 July 1970, R. K. Allen, 1 N exuviae (CAS); same but at Cottonwood, 32 N (CAS); same but at Verde Valley, 26 N (CAS); Oak Creek near Cornville, 18 July 1970, R. K. Allen, 3 N (CAS); same but at Red Rock Crossing, 17-18 July 1970, 2 N (CAS); New Mexico: Catron Co., San Francisco River at Reserve, 22 July 1970, R. K. Allen, 8 N (CAS); Grant Co., Gila River near Cliff on Hwy. 180, 21 July 1970, R. K. Allen, 1 N (CAS); same but 1 mi. S of Cliff, 14 July 1967, R. and D. Koss, 15 N (PU); East Fork Gila River, 40 mi. N of Silver City, Rt. 527, July 1967, R. D. Koss, 1 F (reared) (PU); same but 40 mi. N of Silver City, Rt. 527 at junction with Gila River, 15 July 1967, 1 M (PU); same but on Hwy. 522, 21 July 1970, R. K. Allen, 9 N (CAS); same but on Hwy. 527, 15 N (CAS); West Fork Gila River on Hwy. 527, 21 July 1970, R. K. Allen, 10 N (CAS); Rio Grande at Hatch, 11 Aug 1977, 78 F, 3700', R. K. Allen, 16 N (CAS); Mexico: Chihuahua, Matachic, 6 July 1947, W. J. Gertsch, 2 N (AMNH); same but 7 July 1947, H. T. Spieth, 2 sub M, 26 N (AMNH, 2 N VPI); same but 8 July 1947, 3 sub M, 6 sub F (AMNH); Balleza Rio, Balleza, 5200', 7 July 1947, C. D. Michener, 1 sub F (AMNH); Carta Blanca, 16 mi. W. of Matchic, 8 July 1947, H. T. Spieth, 1 N exuvia (AMHN); Rio Satevo at Gral. Trias on Hwy. 16, 76 F, 5100', 13 July 1977, R. K. Allen, 14 N (CAS).



Map 9. Distribution of I. intermedia (Eaton).

Isonychia (Isonychia) sicca

(Walsh)

Figs. 12a-b, 40, 70, 71, 106, 107

Baetis sicca Walsh, 1862: 371. Type locality: Rock Island, Illinois, M, F. Type deposition: (M) MCZ; Hagen, 1863: 170; Walsh, 1863: 191.

Siphlurus siccus, Eaton: 1871: 130.

Chirotonetes siccus, Eaton, 1885: 208, In part.

Isonychia sicca, Traver, 1935: 497; Burks, 1953: 112; Provonsha and McCafferty, 1982: 31.

Isonychia manca Eaton, 1871: 134. Type locality: West Texas (Bosque County, Texas), F only. Type deposition: British Museum; McDunnough, 1923: 47; Traver 1935: 492. New Synonymy

Chirotonetes manca, Eaton, 1885: 206, In part.

Chirotonetes sp., Eaton, 1892: 16.

Isonychia sicca manca, McDunnough, 1931: 160; Kimmins, 1934: 351; Spieth, 1941: 93; Allen and Cohen, 1977: 109, In part.

Male Imago:

Body: length 8-16 mm, forewings 8-15 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter transverse bands; ocelli whitish; ocelli elevations purplish-black to black. A black spot between compound eyes and scape; margins of transverse shelf and keel black. Antennae whitish tinged with brown or yellow brown distally.

Thorax: Meso- and metanotum dark reddish-brown to brown. Pleura yellowish, membranes tinged purplish. Prothoracic leg brown, femur reddish-brown to yellowish-brown, often darker brown apically, tibia yellowish-brown, often darker brown basally and apically, tarsi yellowish usually with apex of each segment brown; meso- and metathoracic legs yellowish, tarsi tinged with brown. Wings hyaline with all veins yellowish-brown to blackish-brown, often darker at disc; stigmatic region of forewing whitish.

Abdomen: Terga dark reddish-brown or dark purplish-red or dark reddish orange; terga 1-9 with purplish-black or dark brown bands on posterolateral margins; terga 1-9 usually with anterolateral angles shaded with darker brown; terga 1-9 often with faint lighter middorsal stripe and darker submedian streaks; terga 8-10 sometimes yellowish; terga 2-8 usually with a blackish dash or spot near anterolateral edge. Sterna dark reddish-brown to reddish orange; sterna 2-9 usually with a midventral pair of lighter or darker streaks and spots. Caudal filaments yellowish to whitish with brown articulations basally, but occasionally marking entire filaments. Forceps light brown to reddish-brown. Genitalia as Figs. 12a-b.

Female Imago:

Body: length 10-16 mm, forwings 9-15 mm.

Head: Yellowish to orange; compound eyes often with reddish oblique bands; ocelli whitish to gray; ocellar elevations blackish. Dorsally usually with a pair or single diffuse brownish-red stripe; posterolateral angles of occiput blackish; a blackish bar or spot be low eye and scape, spot usually extending upward and often margining eye anteriorly. Antennae yellowish to brown.

Thorax: Pronotum yellowish often margined with purplish-black; meso- and metanotum yellowish-brown to reddish-brown. Pleura yellowish, membranes purplish. Legs colored as male. Wings hyaline with all veins light brown to brown, often crossveins darker; stigmatic region of forewing whitish.

Abdomen: Terga dark reddish-brown to reddish orange; terga 1-9 with purplish black bands on posterolateral margins; terga 1-9 often with a faint lighter middorsal stripe. Pleural fold margined with purplish-black. Sterna dark reddish-brown to orangish brown; sterna 2-9 usually with midventral light oblique streaks and spots. Caudal filaments yellowish with no distinct dark articulations. Subanal plate usually deeply emarginate.

Egg: Typical of subgenus; knob-terminated coiled threads densely packed on 1 hemisphere and scattered on the other or densely covering most of the chorion (Figs. 70-71).

Nymph:

Body: length 10-16 mm.
Head: Reddish brown to yellowish-brown, with a whitish or yellowish coronal stripe, stripe often mottled with brown or often faint. Antennae yellowish with scape and sometimes pedicel brownish.
Thorax: Nota reddish-brown to yellowish-brown with a middorsal whitish or yellowish stripe; pronotum with 2

pairs of submedian crescentric to bar-like yellowish spots; mesonotum with whitish or yellowish spots anterior and lateral of wing pads, mesonotum often with 2 submedian whitish spots fused with middorsal stripe. Legs brown with yellowish marks; forefemora brown usually with a yellowish basal, median and apical transverse brownish bands, tibia yellowish with wide brown medial transverse bands, occasionally absent, tarsi yellowish or whitish, usually with a apical and subbasal transverse band; tarsal claws with 7-11 marginal denticles. Procoxal gills in tufts of multibranched purplish or whitish filaments.

Abdomen: Terga yellowish-brown to reddish-brown; terga 1-9 usually with a yellowish or whitish middorsal stripe often bordered by darker brown or terga 2, 6 and 7 brown, terga 3 brownish with median brownish blotch; terga 4-5 and 8-9 yellowish-brown; tergum 10 brown posterolaterally, yellowish anteriorly. Sterna yellowish-brown to reddish-brown; sytena 1-9 often with a pair of submedian whitish or yellowish often curved bars and 2 pairs of submedian whitish spots; sterna 1-9 often with brownish anterior brownish spots laterally; sternum 10 often brown. Gill lamella purplish to whitish with a median sclerotized ridge brown; fibrillar portion purplish. Caudal filaments yellow to reddish-brown, darker basally, each filament with a wide submedian brownish transverse band, posterolateral of this band filaments often yellowish to whitish, extreme tip usually blackish.

Diagnosis:

Isonychia sicca is recognized by the following combination of characters: (1) lobes of penes broadly rounded or subtruncate distally, (2) wings hyaline, all veins yellowish-brown to black, and (3) abdominal terga reddish brown to dark purplish red, occasionally dark reddish orange.

The nymphs show much variability in coloration, making it difficult to separate them from the other members of the complex, *I. campestris* and *I. edmundsi*, except by geography.

Discussion:

The southwestern subspecies *manca* was differentiated from the midwestern *sicca* by McDunnough (1931) and Traver (1935) by crossveins heavy and black and foretarsus usually fully as long as the tibia. By examining large series throughout the species range including typical manca (especially Texas) and typical sicca (Illinois and Indiana) it was found that both forms are virtually identical as imagoes, differing only in intensity of body and venation color. Like other geographically widespread species of Isonychia, characters such as foretarsal: tibia ratio (ranging from .66-1.20 in single populations examined) and venation color (ranging from yellowish-brown to black in single populations examined) were too variable to recognize the subspecific status of manca. Further collecting will probably indicate that I. sicca ranges from Mexico to Minnesota. There are no confirmed records for I. sicca from northeastern North America. Traver's (1932) North Carolina and Ide's (1930) Ontario records were I. bicolor.

It is interesting to note that the seemingly disjunct northwestern Florida populations (Apalachicola River) are more similar to the midwestern populations of I. sicca than the southwestern populations.

Recently Provonsha and McCafferty (1982) described the nymph of I. sicca from Indiana. Most nymphs of I.

sicca that I examined were more like as those illustrated by Allen and Cohen (1977) for *I. sicca manca*. It would be interesting to study the nongenetic factors such as life cycle and ecological parameters that control these apparent phenotypes.

Biology:

Grant and Stewart (1980) studied the life history of *I. sicca* in an intermittent stream in northeastern Texas. There was at least two generations. Diapause apparently occurred in the egg stage through the dry summer or fall months. They reported that cool water temperatures in the winter probably induced quiescence with eggs hatch resuming again in the spring.

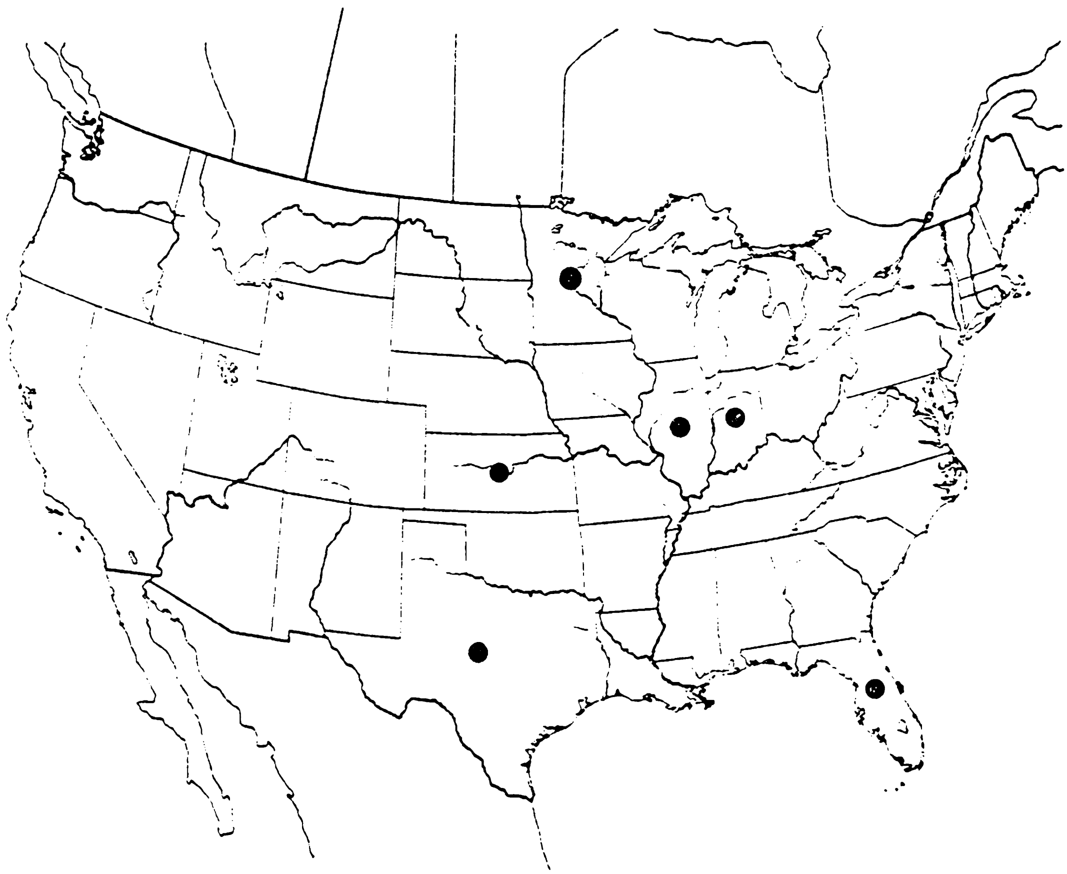
Provonsha and McCafferty (1982) collected *I. sicca* in Indiana from large to moderate fast flowing rivers having rocky substate. It was commonly collected in association with *I. bicolor*.

Material:

Syntypes (?) 2 F, *Isonychia manca*, Texas: Bosque Co., Belfrage, (MCZ# 11256); Holotype M, *Isonychia sicca* Illinois: Rock Island, (MCZ# 11248); Allotype F, same data as Holotype, (MCZ).

Florida: Liberty Co., Apalachicola River at Hwy. 20, Bristol, 29 May 1972, P. H. Carlson, 5 M (FAMU); same but 14 June 1972, 9 M (FAMU); same but 17 June 1972, 6 M, 10 F (FAMU); Illinois: Carroll Co., Mississippi River at Savanna, 19 July 1892, Forbes et al., 2 M (INHS); E. Dubuque, at light, 21 July 1927, T. Frison and R. DG., 5 F (INHS); Fulton, 20 July 1927, T. F. and R. D. G., 1 M, 11 F (INHS); Harrisburg, 16 Aug 1937, ?, 1 M (INHS); Havanna, 28 April-1 May 1898, ?, 1 F (INHS); same but Quiver Lake, 25 June 1884, F. Smith, 3 F (INHS); Homer Park, 30 June 1925, T. Frison, 1 F (INHS); Lake Michigan, Chicago, Lincoln Park, 15 Oct 1881, ?, 1 F (INHS); Mississippi River near Foster, 4 July 1939, B. Berger, 1 M (INHS); Mt. Carmel, 30 June 1906, ?, 3 F (INHS); Oregon, 9 July 1925, T. H. Frison, 1 M (INHS); Quincy, 30 July 1898, ?, 1 F (INHS); Savannah, Mississippi River, 19 July 1892, Forbes et al, 1 M (INHS); same but 27 July 1892, 1 F (INHS); same but 29 July 1892, 1 F (INHS); Rock Island, 1 M (MCZ); Indiana: Wabash River, New Harmony, 16 Jun 1936, H. T. Spieth and Pence, 3 M (AMNH); Posey Co., Wabash River, at old dam, New Harmony 12 Aug 1974, A. V. Provonsha and L. Dersh, 1 M (reared), 9 N (PU); Iowa: Davenport, 5 July 1928, G. S. Walley, 1 F (CNC); Kansas: Lawrence, 1 Aug 1930, L. W. Brown, 1 M, 1 F, (CNC); Kiowa Co., 5 July 1923, R. H. Beamer, 1 M (UK); Russell Co., Saline River, 5 mi. N, 0.6 mi. W of Russell, UV light, 26 June 1978, P. Liechti, 9 M, 3 F (PL); Minnesota: Brown Co., Minnesota River, Kettner's Landing along Co. Rd. 10, N. Potthoff, 1 M (PN); Texas: Caldwell Co., Guadalupe River, 12 mi. S Luling on Hwy. 80, 9 Aug 1970, R. K. Allen, 14 N (CAS); San Marcos River, 6 mi. NE of Luling off Hwy. 80, 9 Aug 1970, R. K. Allen, 1 N (CAS); Denton Co., Clear Creek, Hwy 2450, Bolivar, 16 June 1976, P. M. Grant, 1 M (reared) (FAMU); same but 30 April 1977, 1 M, 2 F (reared) (FAMU); same but 8 May 1977, 1 M (reared) (FAMU); same but 17 May 1977, 4 M, 1 F (reared) (FAMU); same but 30 May 1977, 1 F (FAMU); same but Hwy. 2164, 19 June 1977, 1 M (reared); same but 16 June 1978, 1 F (reared) (FAMU); Nacadoches Co., Angelina River on Hwy. 21 near Douglass, 11 Aug 1970, R. K. Allen, 2 N (CAS); Tom Green Co., Tweedy Ranch, 3 May 1980, B. Henry, 3 N (BH); same but 8 mi. E of San. Angelo, light trap, 13 Aug 1980, B. Henry, 1 M, 2 F (BH): same but Christoval, 23 Oct 1980, B. Henry, 1 M

(BH); Uvalde Co., Rio Sabinal at Utopia, 2 Aug 1970, R. K. Allen, 13 N (CAS).



Map 10. Distribution of _I_. _sicca_ (Walsh).

Diversa Group

Male Imago:

Genitalia: Base of penes broad, constricted ca. 3/4 of length, with posterolateral margins of dorsal lobes rounded giving penes a mushroom-like appearance (Fig. 13).

Isonychia (*Isonychia*) *diversa*

Traver

Fig. 13

Isonychia diversa Traver, 1934: 244. Type locality: Knoxville, Tennessee, M. Type deposition: (M) CU; Traver, 1935: 489; Burks, 1953: 111.

The following description is quoted directly from Traver (1934):244, since no additional material was available other than the type:

Body: length: 9 mm, forewings 9 mm.
Head and thorax reddish brown, brightest on the notum. Pleura somewhat paler.
Legs: Forefemur dark red, becoming blackish at the apex. Tibia almost black. Tarsus pale reddish-brown,

the basal half of the first and second joints yellowish. Foretarsus as long as the tibia. Middle and hind leg whitish, femora slightly tinged with reddish, the claws pale smoky.

Wings: Hyaline. Venation wholly pale.

Abdomen: Smoky brown with a reddish-brown tinge; paler on the middle sternites, which are somewhat translucent. Tergites 9-10 dark red-brown, sternites 8-10 bright reddish. Each segment has a prominent dark brown posterior margin. The pleural fold is narrowly pale on the extreme margin, above which pale line is a narrow dark reddish strip at the center; a small dark mark is present at the stigmatic area. Mid-dorsal line pale; very narrow on the basal segemnts, increasing in width posteriorly. Dark brown wedge-shaped submedian streaks bound it on each side; these are obscure basally, well marked apically. Laterad of each dark streak is another translucent strip, followed by a darker one. Postero-lateral angles reddish brown, antero-lateral angles paler, translucent. Sternites marked similarly to the tergites, with a rather wide pale median stripe and alternating dark and light stripes on each side.

Tails: White unmarked.

Genitalia: Forceps base reddish; deeply excavated on its apical margin. Forceps pale. Penes difer from all other known species of this genus, and are somewhat reminiscent of the genus Siphloplecton. United to form a broad base, they are suddenly incurved and then curve outward again form more or less rounded apical lobes, which are separated by a median V-shaped notch. Each lobe bears a slight indentation on its apical margin. The long second joint of the forceps is at least a third longer than the two terminal joints together. The basal joint is relatively longer and slender.

Female Imago: Unknown

Nymph: Unknown

Discussion:

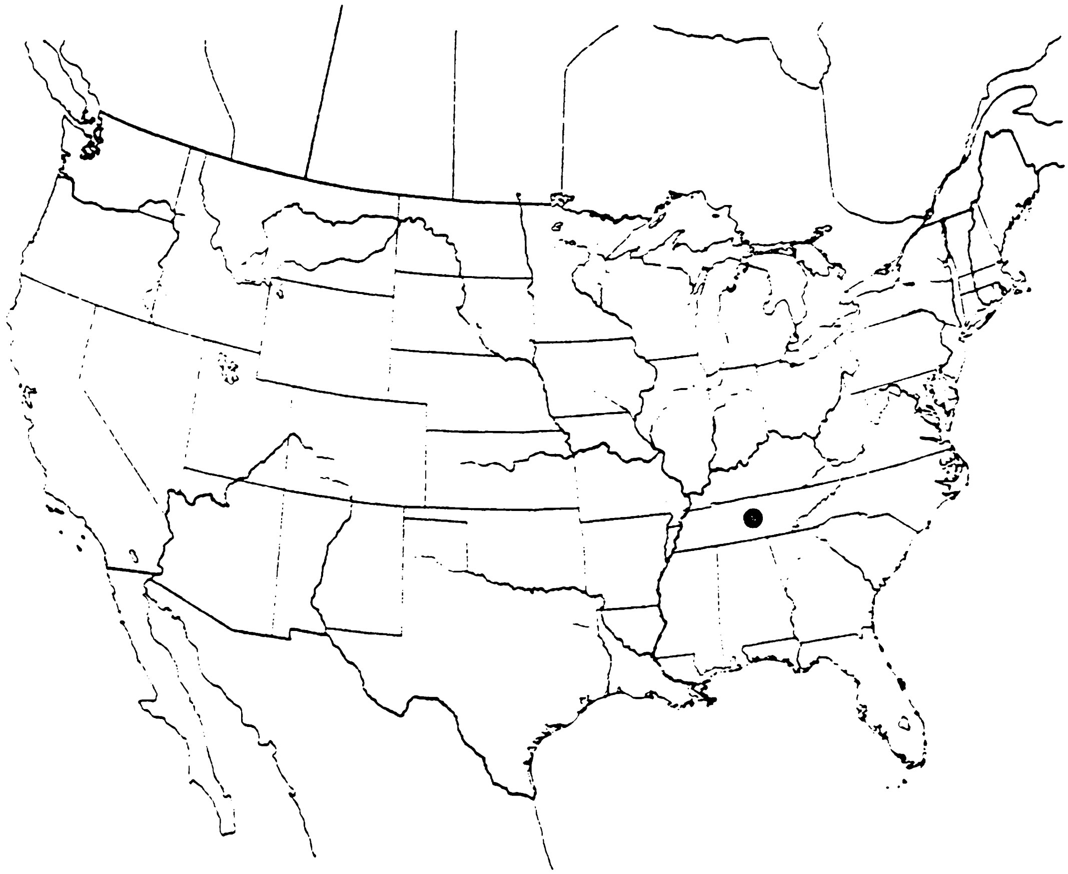
The "mushroom-like" penes readily distinguishes males of this species from all other North American Isonychia. This species is currently known only from the holotype male from Knoxville, Tennessee collected by Dr. Ainslee. There is an additional subimago male also collected by Dr. Ainslee presumably at the type locality about 3 weeks later. Traver (1934) did not include it as a paratype nor a female imago also apparently from the same locality and time. This badly damaged specimen is similar to females of the sicca and bicolor groups.

Biology: Unknown.

Material:

Holotype M, Tennessee: Knoxville, at light, 30 June 1916, G. Ainslee (CU# 1253).

Same as Holotype but 19 July 1916, 1 sub M (CU).



Map 11. Distribution of _I._ _diversa_ Traver.

Subgenus _Prionoides_ Kondratieff and Voshell, In press.

Type species: _Isonychia georgiae_ McDunnough

Male Imago:

Body length 9-17 mm, forewings 9-16 mm.

Abdomen: Yellowish or orangish-brown with dark median and submedian maculae or dark brown with yellowish anterolateral spots.

Male genitalia: Subgenital plate with a broad or only a slight posteromedian emargination (Fig. 15e). Forceps sometimes appearing 5-segmented; penes, dorsally with incurved medial flap with prominent sclerotized lateral and marginal serrations and large spines (Figs. 14-19); usually with sclerotized acute anterolateral spines or projections.

Female Imago:

Body length 9-17 mm, forewings 10-16 mm.

Subanal plate: A shallow or no posteromedian emargination (Figs. 20-22).

Eggs: Biconvex usually with knob-terminated coiled threads closely spaced at center of one side (Figs. 75-95), one species with entire chorionic surface mesh-like with knob-terminated coiled threads uniformly spaced between ridges (Figs. 73- 74).

Nymph:

Abdominal gill lamella without stout spines on apical margin (Figs. 47 and 108). Procoxal gill a single robust purplish filament (Fig. 103), except in *I. sayi*, coxal gill as tuft of multibranched filaments.

Diagnosis:

Male and female imagoes are easily distinguished from *Isonychia* s.s by any of the following characters: (1) subgenital plate with no or only a shallow posteromedian emargination, (2) penes armed dorsally with stout spines and serrations, (3) subanal plate with no or only a slight posteromedian emargination, and (4) biconvex eggs.

Mature nymphs are distinguished by lack of spines on the apical margin of the abdominal gill lamella and usually possessing a single gill filament at the base of each forecoxa (except *I. sayi*).

Specimens of this subgenus are usually absent or rare in most of the large mayfly collections examined. Adults of most of these species are not readily collected in the field by light trapping or sweeping. Specimens are best obtained by rearing nymphs.

Biology:

Generally most of the members of this subgenus are apparently univoltine, inhabiting relatively fast flowing Appalachian or upper Piedmont streams that are clear and cool. Apparently only _I. sayi_ has reached into the midwestern and extreme southeastern parts of North America.

Key to Male Imagoes
of the Subgenus *Prionoides*

1. Caudal filaments brownish with or without dark articulations *or* caudal filaments whitish or grayish to light brown with dark articulations; venation dark brown to purplish black; genitalia as Figs. 14-16 and 18-19 - 2

   Caudal filaments whitish with no dark articulations, venation whitish; genitalia as Fig. 17 - - - - - - - - - - - - - - - *sayi* Burks

2. Caudal filaments whitish or grayish, sometimes basal portion shaded with brown, entire filament including basal portion marked with distinct dark articulations - - - - - - - - - - - - - - - - - - - 3

   Caudal filaments brownish or basally brown becoming paler distally; distal portion may be marked with distinct brownish articulations, basal portion usually not marked with distinct dark articulations - 4

3. Mesothoracic femur distinctly shaded distally with purplish brown (females only known) - *notata* Traver

   Mesothoracic femur not distinctly shaded with purplish brown; male genitalia as Figs. 15a-g - - - - - - - - - - - - - *georgiae* McDunnough

4. Caudal filaments 1/2 to 2/3 brown basally, becoming paler distally, paler portion marked with distinct reddish brown articulations - - 5

   Caudal filaments brown without dark articulations, sometimes paler at extreme distal end - 6

5. Genitalia as Figs. 16a-e, penes with acute and usually toothed distal projections; penes with subterminal notch or emargination - obscura Traver

   Genitalia as Figs. 19a-b, penes rounded anterolaterally, lacking subterminal emargination - - - - - - - - - - - - - - - - similis Traver

6. Genitalia as Figs. 18a-b, incurved portion of penes saw-like, with at least 6-10 large serrations; submedian dorsal marks absent on abdominal terga 1-9 - - - - - - - - - - - - - - - - - - serrata Traver

   Genitalia as Fig. 14, incurved portion of penes not saw-like, with only 2-4 large serrations; submedian dorsal marks present on abdominal terga 1-9 - - - - - - - - - - - - - - - - - distincta n. sp.

Key to Female Imagoes

of the Subgenus _Prionoides_

1. Caudal filaments brown with or without dark articulations _or_ caudal filaments whitish or grayish to light brown with dark articulations; venation dark brown to purplish black; abdominal terga orangish to light yellowish-brown marked with median and submedian brown to purplish-black maculae usually bordering a paler middorsal stripe - 2

   Caudal filaments whitish with no dark articulations, venation narrowly dark brown or purplish; abdominal terga dark brown with large yellowish anterolateral spots - - - - - - - - - - _sayi_ Burks

2. Caudal filaments whitish or grayish, sometimes basal portion shaded with brown, entire filament including basal portion marked with distinct dark articulations - - - - - - - - - - - - - - 3

   Caudal filaments brownish or basally brown becoming paler distally; distal portion may be marked with distinct brownish articulations; basal portion usually not marked with distinct dark articulations - 4

3. Mesothoracic femur distinctly shaded distally with purplish brown - _notata_ Traver

   Mesothoracic femur not distinctly shaded with purplish brown - _georgiae_ McDunnough

4. Caudal filaments brown basally, becoming paler distally, paler portion usually marked with reddish brown articulations - _obscura_ Traver and _similis_ Traver

Caudal filaments brownish without dark articulations, sometimes paler at distal end - 5

5. Submedian dorsal marks absent or obscure on abdominal terga 1-9 - *serrata* Traver

Submedian dorsal marks present and distinct on abdominal terga 1-9 - *distincta* n. sp.

Isonychia (*Prionoides*) *distincta*

new species

Figs. 14, 23a-b, 73, 74

Male Imago:

Body: length 11-14 mm, forewing 11-14 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter transverse band; ocelli white; ocellar elevations blackish. Antennae brownish. Sides of transverse shelf of yellowish to white. Remnants of maxillary palps purplish.

Thorax: Mesonotum brown; metanotum dark brown. Pleura light brown. Prothoracic leg brown, femur light brown to whitish basally; meso- and metathoracic leg whitish, tarsi lightly tinged with purple. Wings hyaline with all veins dark brown to purplish-black; forewings with a light brownish stain in stigmatic region, few stigmatic crossveins anastomosed.

Abdomen: Terga 1-9 yellowish with wide reddish-brown bands on posterior margins, each band diffusely extending anteriorly; these bands interrupted medially by a yellowish to orangish middorsal stripe (Fig. 23a-b). middorsal stripe bordered laterally by dark brown streaks or blotches; stripe sometimes divided by diffuse brownish pigment posteriorly or partly obscured by brown shading (Fig. 23b); terga 2-9 with brown submedian oblique marks to crescent bars; terga 2-8 with black lines or spots just below pleural fold near each spiracle; terga 10 yellowish. Sterna 1-9 reddish-brown with anterolateral yellow spots becoming more prominent posteriorly; pair of anterior pale oblique bars on sterna 1-9. Caudal filaments uniformily brown, lighter at extreme tip. Forceps brown. Genitalia as Fig. 14.

Female imago:

Body: length 10-15 mm, forewings 10-14 mm.
Head: Whitish to yellowish brown; ocelli white; ocellar elevations black. Two black spots at posterolateral angle of occiput. Antennae light brown.
Thorax: Mesonotum light brown; metanotum brown. Legs colored as male, forelegs sometimes darker. Wings hyaline with all veins dark brown to black , forewings with brownish stain in stigmatic region, few stigmàtic crossveins anastomosed.

Abdomen: Terga 1-9 yellowish or very light brown with wide reddish-brown bands on posterior margins, additional light brown diffuse shading usually extending beyond one-half of each tergum to anterior margins, bands interrupted medially by a yellowish middorsal stripe; terga 2-9 with stripe bordered laterally by dark brown blotches; terga 2-9 with dark brown submedian lines to crescentric bars; terga 2-8 with a distinct black spot just below pleural fold near spiracle; tergum 10 yellowish. Sterna 1-9 reddish-brown with anterolateral yellow areas becoming more prominent posteriorly; pair of anterior light oblique bars and spots on sterna 2-7(8). Caudal filaments uniformly brown, lighter at extreme tip. Subanal plate very shallowly emarginate posteriorly or straight.
Egg: Biconvex, entire chorionic surface mesh-like with knob terminated coiled threads uniformly spaced between ridges, lacking marginal carina (Figs. 73-74).

Material:

Holotype M, allotype F: Tennessee, Fentress County, Burrville, 16 June 1957, L. Berner (3951.0).
Paratypes: Same 1 M, 3 F.

The holotype, allotype and 2 female paratypes will be deposited in the Florida State Collection of Arthropods, Gainesville. One male and 1 female paratype deposited in the VPI&SU Collection.

Dr. Berner's original label states that Burrville is in Fentress County, however it is in Morgan County, Tenneessee. He listed these specimens as *I. serrata* in Berner (1977).

Eytmology:

The specific epithet refers to the atypical and unique eggs of this species of *Prionoides*.

Diagnosis:

Male imagoes of *I. distincta* are very similar to *I. georgiae* but may be distinguished by the following combination of characters: (1) Caudal filaments uniformly brown, paler at extreme distal tips; entire filament with no darker brown marked articulations, and (2) distinctive eggs.

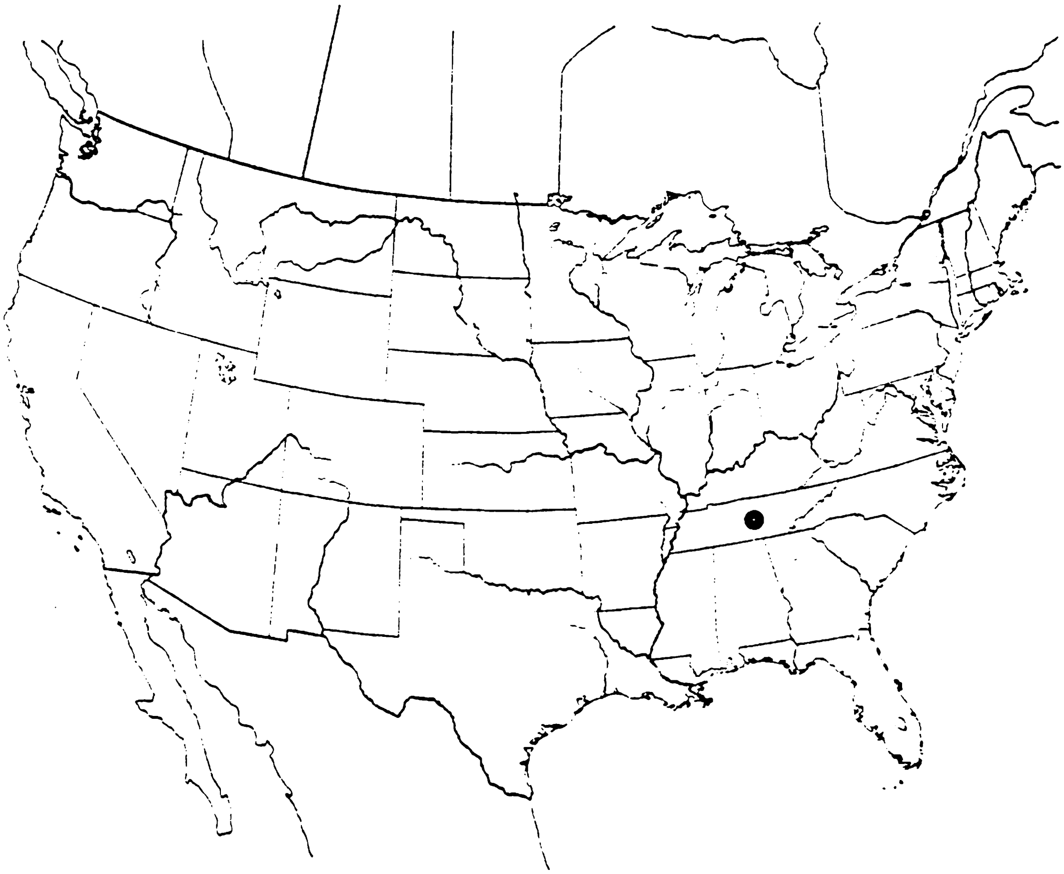
Discussion:

Female imagoes may have the extreme tips of the caudal filaments with several darker marked articulations. The eggs of this species are very atypical of all other known species of Prionoides. The entire chorionic surface has a mesh-like reticulation with the knob-terminated coiled threads uniformly spaced between the ridges. The egg is biconvex but not as compressed as the other species of Prionoides (Fig. 73), lacking the usually well defined marginal carina (Fig. 72). The knob-terminated threads are also present on both sides.

A single male imago from Pennsylvania (Butler County, North Branch Slippery Rock Creek, 1 mile East northeast of White Oak School, White Oak Road, 25 June 1967, J. W. Richardson, Jr. coll., UU) may belong to this species. It has light brownish tinting in the disc area of the forewings. It was not considered a paratype since these were no associated females and only a single specimen was available from a rather disjunct geographical locality (north of Pittsburgh, PA).

Biology:

No nymphs are presently known. The adults were collected in mid-June, typical for several species of *Prionoides*.



Map 12. Distribution of I. distincta n. sp.

Isonychia (*Prionoides*) *georgiae*

McDunnough

Figs. 15a-g, 20, 44a-b, 75-80, 103

Isonychia georgiae McDunnough, 1931: 159. Type locality: Rabun County, Georgia, M. Type deposition: (M) CNC; Traver, 1932: 208; Traver, 1935: 490.

Isonychia annulata Traver, 1932: 204. Type locality: Big Alamance Creek (Guliford County?), North Carolina, M, F and nymphs. Type deposition: (M) CU; Traver, 1935: 484. New Synonymy

Isonychia thalia Traver, 1934: 253. Type locality: Davidson River, Transylvania County, North Carolina, M, F and nymphs. Type deposition: (M) CU; Traver, 1935: 499. New Synonymy

Male Imago:

Body: length 10-15 mm, forewings 10-15 mm.
Head: Eyes rust brown to gray (reddish in life) with dorsal portion separated by lighter transverse bands; ocelli whitish or gray; ocellar elevations blackish purple. Antennae yellowish to brownish tinged with purple, distally often whitish. Sides of transverse

shelf yellowish. Black mark below compound eye at anterolateral edge. Remnants of maxillary palps purplish.

Thorax: Mesonotum yellowish brown to brown; metanotum brown. Pleura yellowish with brown and purplish tinting. Prothoracic femur brown, yellow to yellowish brown basally, joint between femur and tibia yellowish, tarsal segments light brown to purplish-gray; mesothoracic legs whitish or yellowish; tarsal segments slightly tinged with purple, claws tinged with purple. Wings hyaline with all veins brown to purple; forewings with whitish stain in stigmatic region, few stigmatic crossveins anastomosed.

Abdomen: Terga 1-9 orangish to light brown, purplish-black bands on posterior margins, each band interrupted dorsomedially by an indistinct middorsal light brown stripe; terga 2-9 stripe bordered laterally by purplish-brown streaks or blotches; terga (1)2-8(9) with submedian purplish-brown oblique or crescent streaks or blotches; terga 2-9 with extreme posterolateral areas whitish or yellowish; tergum 10 yellowish. Black dash just below pleural fold near each spiracle. Sterna 1-9 orangish-brown to yellowish, with anterior sterna often darker. Sterna 2-6(7) with a pair of midsternal indistinct difffuse purplish-brown triangular areas, often becoming bar-like on sterna 7-9; sterna 2-9 often with indistinct whitish or light brownish transverse dots; sterna 2-9 with purplish bar paralleling pleural fold. Caudal filaments usually whitish gray to very light brownish yellow with distinct reddish-brown to dark brown articulations marking entire filaments; basal portion of filaments often shaded with reddish-brown, occasionally entire filaments brownish with distinct darker brown articulations. Forceps purplish-brown. Genitalia with penes variable in structure (Figs. 15a-g).

Female Imago:

Body: length 10-16 mm, forewings 10-15 mm.
Head: Yellowish to orangish; ocelli whitish to gray; ocellar elevations blackish purple. Antennae purplish-brown; flagella often whitish to purplish. Posterior lateral angles of occiput purplish-black; blackish streak or spot below compound eye at anterolateral edge. Remnants of maxillary palps purplish.

Thorax: Mesonotum yellow; metanotum yellowish, often tinged with purple. Pleura yellowish with membranes purplish. Legs colored as male. Wings hyaline, all veins purplish-brown; forewings with whitish stain in stigmatic region.

Abdomen: Terga 1-9 yellowish orange with an indistinct to obscure yellowish middorsal stripe; terga 2-9, stripe interrupted by purplish-black bands on posterior margins; terga 2-9 stripe bordered laterally by purplish black streaks or blotches; terga 2-9 with submedian purplish-brown or black streaks or crescentric spots. Tergum 10 yellowish. Purplish black dash below pleural fold. Sterna 1-9 yellowish to light orangish-brown; sterna 1-9 with light purplish or black bands on posterior margins; sterna 2-10 or 2-7 with a pair of midventral faint purplish-brown triangular to bar-like areas, often more distinct on anterior segments. Dots as male often present. Egg valves often with purplish-brown spots on each of posterior margin; sterna 1-9 with a purplish bar paralleling pleural fold. Caudal filaments as male. Subanal plate tinged with purple and usually entire or slightly emarginate.

Eggs: Typical of subgenus (Figs. 75-80).

Nymph:

Body length 11-17 mm.

Head: Brown with whitish coronal stripe. Antennae white, scape and pedicel brownish, flagella with brown transverse band 1/3 distance from scape.

Thorax: Nota brown often with a middorsal whitish stripe, most distinct on mesonotum. Pronotum usually with 2 pairs of submedian crescentric or bilobed marks; small whitish spots and streaks anterior and lateral of mesothoracic wing pads; a pair of medial whitish spots on mesonotum. Legs brown with whitish markings, forefemora brown with whitish basal, submedian and apical transverse bands; tibia whitish with a median brownish transverse band; tarsi whitish with a median transverse band; tarsal claws with 5-10 marginal denticles. Procoxal gill a single robust purplish filament.

Abdomen: terga brown; terga 1-9 with or without a yellowish or very light brown middorsal longitudinal stripe; stripe often with blackish or brownish medial longitudinal dashes. Color pattern of adult usually visible. Terga 1-9 with a pair of submedian whitish dots or streaks; terga 1-9 with a whitish spot near posterolateral edge; terga 10 whitish anteriorly , brownish posteriorly. Sterna yellowish brown; sterna 1-9 with a submedian whitish or yellowish pattern as Fig. 44; color pattern of adult usually visible (sterna 1-9 with 4 purplish-brown submedian blotches or bars and sterna 1-9 with a blackish spot near lateral edges). Gill lamella with a large often diffuse purplish spot, two brownish purple spots in distal margin; median sclerotized streak brown; fibrillar portion purplish. Caudal filaments brown, distally whitish, tinged with black at extreme tips.

Diagnosis:

Isonychia georgiae may be distinguished by the following combination of characters (1) caudal filaments usually whitish gray to very light brown with distinct reddish-brown to dark brown articulations marking entire filaments, occasionally filaments brownish but still marked with dark brown articulations, (2) mesothoracic tibiae yellowish, and (3) male penes as Figs. 15a-g. The nymphs are very similar to *I. obscura* but may be usually separated by the abdominal sternal pattern (Fig. 44).

Discussion:

The confusion in denomination of this species is due to the original brief description of *I. georgiae* by McDunnough (1931), Traver's (1932) apparent redescription, Traver's (1934) naming of *I. thalia*, for her 1932 specimens, and again the redescription of the apparent "true" *georgiae* by Traver (1935). McDunnough (1931) described *I. georgiae* from a single male specimen from Rabun County Georgia. This pinned specimen is damaged, with the abdomen fragmented and caudal filaments missing. McDunnough's description was very brief, significantly omitting any reference to the caudal filaments, perhaps indicating that they were already missing at that time. The very characteristic dorsal abdominal pattern of median and submedian maculae are not clearly ascertainable with dry and pinned material as compared to well preserved alcohol specimens. This may also account for his brief description. Traver in 1932 thought she reared the true *georgiae* from the Davidson River (Transylvania

County, North Carolina). She completely described all stages, although her material only consisted of one male imago, one female imago and one female nymph. However, after receiving specimens (apparently one male and one female imago) from Dr. Fattig from Town Creek (Cleveland County, Georgia) she renamed her original Davidson River material thalia because of "distinct" differences in size and coloration of the abdomen and "slight differences in the genitalia."

Traver (1935) redescribed again the apparently "true" georgiae from Dr. Fattig's material. She stated that georgiae had a dark wine red abdomen and only trace of submedian lines. The Fattig specimens were examined. The male is badly damaged, the female is in fair condition. Traver probably based most of her description on the female. This female is void of eggs. In Prionoides females which have voided their eggs have a much more pronounced reddish tinge to the abdomen and therefore the abdominal maculae are indistinct. The eggs being whitish to yellowish give the distinctive yellowish orange ground color accentuating the maculae patterns.

I collected and reared _I_. _georgiae_ from Town Creek (Cleveland County, Georgia) and they were the same as Traver's Davidson River material, the only discrepancy being the coloration of the caudal filaments- "greyed purplish-brown and joining slightly darker" (Traver 1932 as _I_. _georgiae_) rather than grayish to yellowish brown with distinct brownish articulations. I also collected and reared adults from the Davidson River and found that indeed these specimens were typical _I_. _georgiae_ in all respects including the caudal filaments (grayish to yellowish brown with distinct brownish articulations). Careful examination of the types of _thalia_ revealed apparently pale caudal filaments with dark articulations. However, this material has been preserved for over 50 years in alcohol and the "purplish-brown" color may have faded. However in a series of typical _I_. _georgiae_ adults reared and collected by light trap from the Cullasaja River (Macon County, North Carolina) several male imagoes had caudal filaments dull brownish, somewhat darker basally, lighter distally, but brownish articulations did mark entire filaments. This seems to indicate that _I_. _georgiae_ usually has grayish to yellowish brown caudal filaments with distinct brownish articulations (basal portion often shaded with reddish-brown), but *thalia* like individuals do occur with filaments colored as above. The male penes of *I. thalia* (Traver's original 1934 Fig. 11 is erroneous, see Figs. 15b and 15d) falls well within the range of *I. georgiae*. All of the above evidence indicates that *I. thalia* is the same as *I. georgiae*, and we place it as a junior synonym of *I. georgiae*.

Isonychia annulata was originally described from one male imago, one female imago and a male subimago from Big Alamance Creek South of Greensboro, North Carolina. We collected and reared a large series of both male and female imagoes from this creek. Examination of these adults and nymphs and the types clearly indicated that *I. annulata* is a junior synonym of *I. georgiae*. The male genitalia of *I. annulata* fall within the range of variablity observed with *I. georgiae*.

In the series of reared adults from Big Alamance Creek no "very faint brownish cast" in the basal and central region of the forewing was detected. Individual male imagoes were allowed to remain alive for more than 3 days and there was no additional color development. The large "whitish" blotches on the abdomen are more evident on female imagoes only after a period of preservation in alcohol. In live and freshly preserved individuals, the abdominal ground color is orangish-brown in the male and yellowish orange in the female, fading to light yellow to whitish in alcohol.

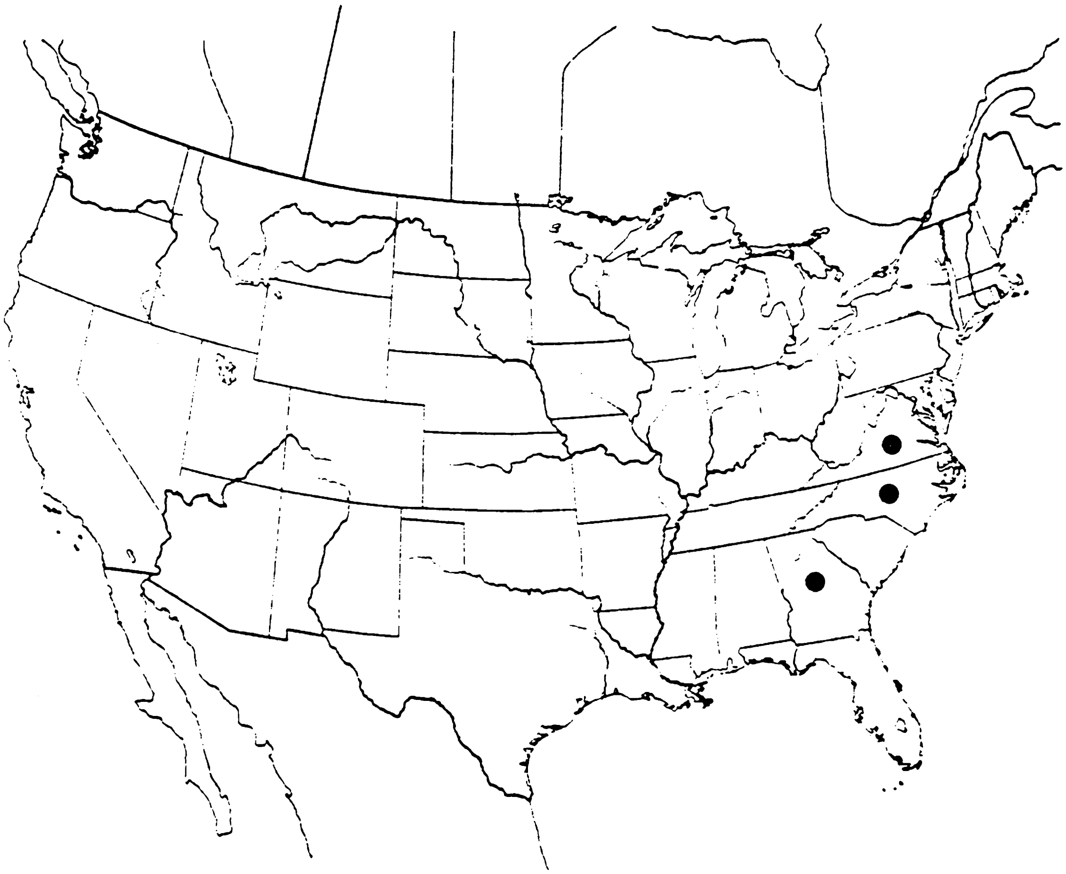
Biology:

I. georgiae has been collected from 4th - 5th order Appalachian to Piedmont streams. Big Alamance Creek is a typical 4th order North Carolina Piedmont stream with substrate mostly pebble (16-64mm) with some cobble (64-256mm), overlying bedrock. Maximum water temperature recorded at this site was 28 C. *Isonychia georgiae* is univoltine in this creek with maximum emergence in the first week of June. *Isonychia bicolor* was also abundant at this site. Town Creek is a rather large and silty stream with mostly sand (0.25-0.5mm) and pebble (16-64mm) substrate. *Podostemum ceratophyllum* Michaux, river weed, grows sparsely in riffle areas. Stream temperature at time of collection of nymphs was 26 C. Good populations of this species also occurred in the Cullasaja River (water temerature 21 C at time of maximum emergence) and the Davidson River (water temperature was 22 C at time of moderate emergence). This species is the most wide spread of all Prionoides species and can apparently tolerate a variety of stream conditions.

Material:

Holotype M, Isonychia georgiae, Georgia: Rabun Co. (CNC# 3250); Holotype M, Isonychia annulata, North Carolina: Big Alamance Creek, 22 May 1929, JRT (CU# 1088.1); Allotype F, same (CU# 1088.2); Paratype sub M, same (CU# 1088.3); Holotype M, Isonychia thalia, North Carolina: Davidson River, 9 July 1930, JRT (CU# 1259.1); Allotype F, same but 21 July 1930, JRT (CU# 1259.2); Paratype N, same but 27 June 1930, JRT (CU# 1259.3).

Georgia: White Co., Town Creek, 1.5 mi off Rt. 115 near Cleveland, 8 July 1981, 1981, BCK, 3 M, 2 F (reared), 8 N (VPI); North Carolina: Guliford Co., Big Alamance Creek, Co. Rt. 1005, 23 May 1981, BCK, 1 sub F (reared), 37 N (VPI); same but 3 June 1981, 11 M, 9 F (reared), 3 N (VPI); Macon Co., Cullasaja River, Co. Rt. 1672, 7 July 1981, (BCK), 6 M (2 reared), 9 F (reared), 19 N (VPI); Transylvania Co., Davidson River, St. Rt. 276 near Gov. Rd, 8 July 1981, BCK, 2 M, 3 F, 2 sub F (reared) (VPI); Polk Co., Pacolet River, St. Rt. 176 near Co. Rt. 1102, 9 July 1981, BCK, 1 F (reared), 9 N (VPI); Virginia: Louisa Co., South Anna River, St. Rt. 522, 12 June 1978, BCK, 9 N (VPI).



Map 13. Distribution of Isonychia georgiae McDunnough.

Isonychia (*Prionoides*) *notata*

Traver

Figs. 22, 81, 82

Isonychia notata Traver, 1923: 210. Type locality: Bald Creek, Yancey County, North Carolina, F and nymph. Type deposition: (F) CU; Traver, 1935: 493.

The following description is taken directly from Traver (1932): 211-212 since no additional material was available other than the type:

Body: length 13mm, forewings 12mm.
Head: Greenish yellow. Dark purplish spot in posterior angles of occiput. Antennae purplish. Black spot below lateral carina on each side, another to each compound eye. Compound eyes bluish gray.
Thorax: Pronotum yellowish. Dark purple at center of posterior margin. Lateral borders marked with purplish grey. Mesonotum and pleura greenish yellow. Mesonotal spine faintly marked with lavender, also its lateral aspects. Pleura marked with greyish lavender. Metanotum yellowish brown, purple at center of

posterior margin. A purplish-brown spot on each side of median line at center of sclerite. Ventrally, two dark transverse bars, the anterior one discontinuous, between forelegs. Central sclerite of metasternum brown. Its anterior portion, and the median area of the metasternum, purplish.

Legs: Basal half of fore femur yellowish; distal half purplish-brown, borders darker. Tibia greyed purplish-brown, darker in basal half. Tarsus greyed lavender, joinings and claws darker. Tarsus and distal fourth of tibia of second leg, and last two tarsal joints of third leg, purplish-brown with olive tinge. Other portions of these legs greenish white, the second tibia with a brown stain near each end of the whitish portion.

Wings: Transparent, iridescent. Venation light purplish rose. Stigmatic area opague white. No forking nor anastomosis of cross veins in this area. Some of veins from 1st anal to margin, twice forked.

Abdomen: Dorsally, yellow tinged with light orange; 10th tergite brighter yellow, unmarked. Median light dorsal streak, bordered on each side by a dark purplish-brown line extending the length of the tergite. Posterior border of each tergite dark purplish-brown except at median line. Arising from the posterior margin halfway between the median line and the pleural fold, a light purplish-brown mark, widest at the base, curves forward and outward, not quite attaining the anterior border. Between this and the pleural fold, a crescentric mark of the same color. One end of the crescent is in the pleural fold, the other in the space between this fold and dark line mentioned above. Thus the crescent occupies most of the posterior lateral angle, its open side toward the center of the tergite. Posterior half of pleural fold on each tergite margined with lavender. Ventrally, light yellow. Posterior margin of each sternite purple. On each side of the light median, an interrupted purplish-brown streak, extending the length of the sternite on 1-6, but on 7 and 8 not reaching the posterior margin. Central portion of lip of egg valve reddish purple. Between the longitudinal streaks on 8, a chestnut transverse bar, connected on each side to the outer edge of the egg valve by a short arm. On posterior portion of each sternite, a reddish purple streak borders the pleural fold. In the anterior portion of each, in line with this streak, a dark purple spot. (Subanal plate slightly emarginate, Fig. 22).

Tails: In basal two-thirds, light purplish-brown; distal third greyish white. A short transition between these, light tan. Joinings dark purplish-brown, quite prominent.

Egg: Typical of subgenus (Figs. 81-82).

Nymph: Mature nymph dark reddish-brown, lighter ventrally. Immature nymph deep orange-brown.

Head: Median line of vertex and occiput mottled whitish. White spots laterad of each lateral ocellus, and cephalad of median ocellus. Frontal carina whitish. Antennae dark brown at base, remaining portion yellowish brown, crossed by black transverse band one-third from base.

Thorax: Median line of entire dorsal aspect a wide whitish band, in immature nymph. In mature nymph, whitish band wide at anterior border of pronotum only, becoming narrower until it almost disappears at the mesonotal spine. Crescentric whitish mark on each side of pronotum, not far from median line. Halfway to lateral border, a large white blotch. One or two smaller white dots toward lateral border from this blotch. White spot on each side of median line of mesonotum, between inner margins of wing pads. Several small white spots anterior to wing roots. Pleura and ventral surface light reddish-brown.

Legs: Dark reddish to purplish-brown, with yellowish markings. Tarsi narrowly yellow at basal end, distal half also yellow. Fore tibia narrowly lighter at each, other tibiae with rather wide yellow band distally. Femora yellow narrowly at each end, a wider discontinuous blotch near the center.

Abdomen: Immature nymph with wide dorsal median line. On mature nymph, only the anterior segments are light for their entire length; others light at anterior borders only. A yellowish white streak on each side of median line, arising from the white line near the anterior border, extends beyond the center of the tergite. A white spot on each side at the center, near pleural fold. Tergite 10 yellowish basally, blackish brown distally. Ventrally, each ganglionic area is a large white blotch, from which extends on each side a white line outwards and backwards to the center of the sternite. Four white dots arranged transversely at

center of each sternite. On posterior sternites, median line posterior to ganglionic area is likewise white. A dark spot near each anterior lateral angle.
Gills: Greyish lavender, the borders and median division brownish. Two purplish-brown spots in the outer margin of each.
Tails: Reddish brown as far as the first black transverse bar.

Diagnosis:

The single female imago apparently may be distinguished by the following combination of characters: (1) distal fourth of mesothoracic tibia purplish-brown and (2) caudal filaments purplish-brown basally, grayish white distally, with entire filaments marked with purplish brown articulations.

Discussion:

This species is still known only from the type female imago and two nymphs. I collected and reared a good series of _Prionoides_ adults from Bald Creek, Yancey County near the town of Bald Creek, North Carolina, the type locality of _I_. _notata_. However, these adults were clearly *I. serrata*. *Isonychia notata* is apparently very similar to *I. georgiae*. Thirty-two females of *I. georgiae* were carefully examined and none had the distal portion of the mesothoracic tibia purplish-brown, a character still very pronounced on the holotype. The two nymphs and other nymphs identified by Dr. Traver were also carefully examined. Many characters useful in separating the various species of *Prionoides* are no longer evident after the many years of preservation. Since the single specimen of *I. notata* may be only a local variant or an aberrant specimen and thus possibly be a synonym of *I. georgiae*, further collecting at the original type locality is required to settle this question. The Swain County, North Carolina female imago listed by Berner (1977) was examined and is probably not *I. notata* but more likely *I. georgiae*.

Material:

Holotype F, North Carolina: Bald Creek, 17 July 1930, JRT (CU# 1087.1).

Isonychia (*Prionoides*) *obscura* Traver

Figs. 16a-e, 45, 83, 102

Isonychia obscura Traver, 1932: 217. Type locality: Penrose, Transylvania County, North Carolina. M. Type deposition (M) CU; Traver, 1935: 494.

Male Imago:

Body: Length 12-15 mm, forewings 11-14 mm.
Head: Eyes purple gray with dorsal portion separated by lighter transverse bands; ocelli grayish; ocellar elevations dark purple to black. Antennae light purplish-brown. Purplish spot below compound eye at anterolateral edge. Remnants of maxillary palps purplish.
Thorax: Meso- and metanotum dark brown. Pleura brownish with membranes purplish. Prothoracic brown, femur lighter basally, tarsal segments light brown; meso- and metathoracic legs whitish to light yellow, tarsal segments tinged with purplish. Wings hyaline with all veins dark brown to dark purple; forewings with whitish stain in stigmatic region.

Abdomen: Terga 1-9 orangish-brown, dark brown bands on posterior margins, each band interrupted dorsomedially by an indistinct reddish-brown middorsal stripe; terga 1-9 with additional diffuse brown shading on posterior one-half; terga 1-9 stripe bordered anterolaterally by dark purplish-brown marks; terga 2-9 with anterolateral dark purplish-brown streaks, terga 2-9 also with posterolateral purplish-brown triangular-like areas; tergum 10 yellowish brown. Pleural fold margined with purplish-brown. Black spot or dash just below pleural fold near each spiracle. Sterna 1-2(3) brown; sterna 3-9 light brown; sterna 1-9 with a faint light median streak; sterna 2-8 a pair of median purplish streak; sterna 2-8 often with posterior margins diffusely banded purplish-brown. Sterna 1-9 with lateral purplish-brown bar paralleling pleural fold; sternum 10 brown. Caudal filaments brown basally, becoming light gray or very light brown distally, this lighter portion marked with reddish-brown articulations. Forceps purplish-brown, last segment often whitish. Genitalia as Figs. 16a-e.

Female Imago:

Body: length 14-16 mm, forewings 14-15 mm.

Head: Yellowish; ocelli whitish to gray; ocellar elevations purplish-black. Antennae purplish-black. Posterolateral angles of occiput blackish; blackish streak or spot below compound eye at anterolateral edge. Remnants of maxillary palps purplish.

Thorax: Mesonotum yellowish brown; metanotum light yellowish brown or light brown. Pleura yellowish with membranes purplish. Legs colored as male. Wings hayline, all veins purplish-brown; forewings with whitish stain in stigmatic region.

Abdomen: Terga 1-9 light orangish-brown with an indistinct yellowish orange middorsal stripe; terga 29 stripe interrupted by reddish-brown bands on posterior margins; terga 2-9 stripe bordered laterally by purplish marks; terga 2-9 oblique purplish streaks laterally, often faint; terga 2-9 with posterolateral purplish triangular areas; tergum 10 yellowish. Pleural fold margined with purple. Purplish black spot just below pleural fold by each spiracle. Sterna 2-9 light reddish-yellow; sternum 1 purplish; sterna 1-9 with a pair of median purplish streaks; sterna 2-8 purplish shading on posterior margins; sterna 2-8 with purplish bar paralleling pleural fold; sternum 10 yellowish. Caudal filaments as male, often entire filaments marked with dark reddish-brown articulations. Subanal plate shallowly emarginate.

Egg: Typical of subgenus (Fig. 83).

Nymph:

Body: length 10-15 mm.

Head: Brown with whitish coronal stripe, brownish moulting around edges. Antennae witish, scape and pedicel brownish, flagella with brownish transverse band ca. 1/3 distance from scape.

Thorax: Nota light brownish to brown, often with a faint whitish middorsal stripe; Pronotum usually with 2 pairs of submedian often bilobed or concentric whitish marks; small whitish spots and streaks anterior and lateral of mesothoracic wing pads; a pair of median whitish spots on mesonotum. Legs light brown with whitish markings, forefemora light brown usually with basal, submedian and apical whitish transverse bands, sometimes bands faint, tibia whitish with a median brownish transverse band, tarsi whitish with a median or basal brownish transverse bands; tarsi claws with 5-11 marginal denticles. Procoxal gills a long single robust purplish filament.

Abdomen: terga yellowish brown; terga 1-9 usually without a distinct lighter middorsal stripe; color pattern of adult usually visible; terga 1-9 with a pair of submedian whitish dots or streaks; terga 1-9 with a whitish spot near posterolaterial edge; terga 10 whitish anteriorly, brownish posteriorly. Sterna yellowish brown; sterna 3-6 with four whitish transverse dots and a pair of concentric-like whitish marks (Fig. 45), often outer pair of dots fused posteriorly with concentric marks; color pattern of adult visible (sterna 2-7 with 2 pairss of midventral purplish-black blotches and usually sterna 1-9 usually with a dash or spot at lateral edges). Gill lamella with a large purple median spot; two brownish purple spots in distal margin. Median sclerotized streak brown; fibrillar portion purplish. Caudal filaments brown, distally whitish, sometimes tinged with black at extreme tips.

Diagnosis:

Isonychia obscura is most similar and closely related to *I. georgiae* and *I. distincta*. Male imagoes may be distinguished by the following combination of characters : (1) caudal filaments brown basally, distally grayish or light brown, this lighter portion marked with distinct reddish-brown articulations, and (2) penes with acute and often "toothed" distal projections with a subterminal lateral notch or emargination. Mature nymphs are very similar to those of *I. georgiae* and usually are distinguished by the abdominal sternal pattern (Fig. 45) Female imagoes cannot be usually separated from *I. similis*. However, apparently, *I. obscura* prefers larger and warmer streams of lower elevations.

Discussion:

An intercalary spine in the subterminal penial notch or emargination is sometimes present, usually only on one side. Series of males examined from a single locality indicated that this spine can be in the membranous portion of the notch or just below or above the notch or emargination (see Figs. 16a-b).

Biology:

This species, originally described from one male imago from North Carolina, is along with *I. georgiae* one of the most common and widely distributed species of *Prionoides*. Large populations occur in several Piedmont and Ridge and Valley 4th and 5th order rivers of Virginia.

The life history and ecology of this species were investigated at the Little River. The river and the sampling site is described under *I. bicolor*.

Subimagoes of *I. obscura* emerged in the late-afternoon to early evening. Unlike most species of the subgenus *Prionoides*, *I. obscura* nymphs did not climb out of the water for emergence. They either migrated to shallow stream margins (2-4cm) and emerged by briefly clinging to the many projecting rocks and debris available or by briefly clinging to large projecting rocks on sides away from the fast current. Subimagoes would fly high into nearby trees.

A small nuptial flight was observed in the early afternoon. A swarm of 10-15 males was rhythmically undulating 10-20 m above a riffle. No copulation was observed. Females were seen flying singly above the water's surface in the later afternoon.

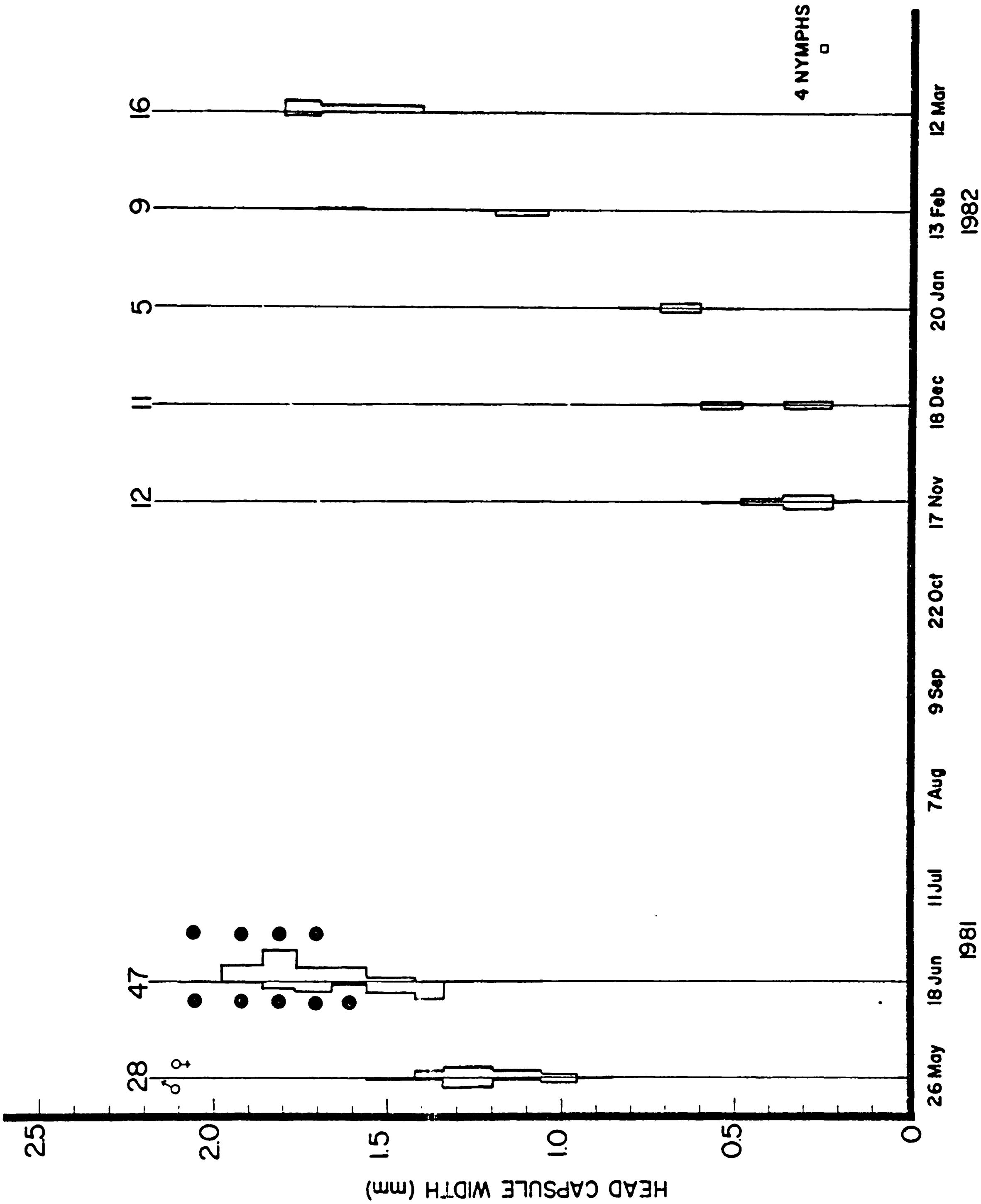


Fig. 5a. Size frequency distribution of head capsule widths of <u>Isonychia obscura</u>. Sex could be determined for nymphs with head widths > 0.9 mm. Black dots denote nymphs with black wing pads; Little River.

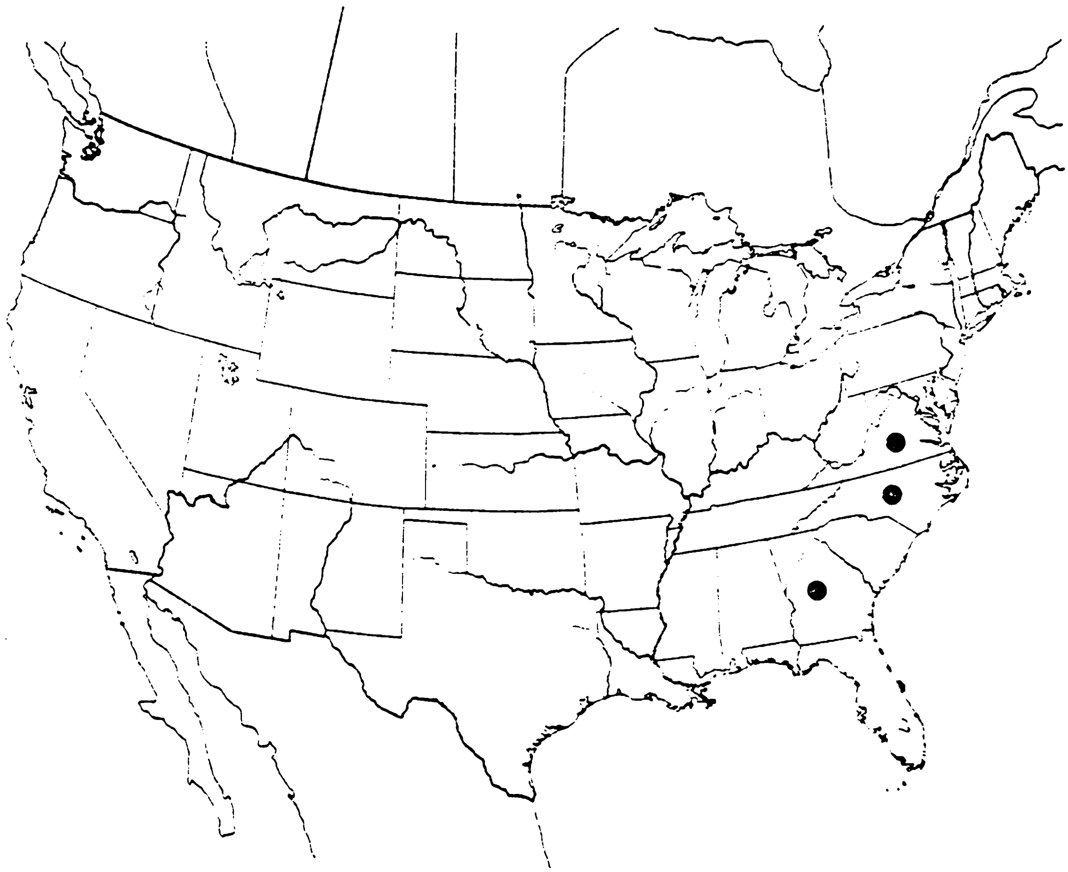
The development cycle was clearly univoltine (Fig. 5a) with all adults emerging in June. Very early instars were again collected in early November, indicating a egg diapause during the warmer months. Egg hatching correlated with temperatures dropping below 15°C (Fig. 115). Most species of the subgenus *Prionoides* are apparently adapted to cooler streams than species of *Isonychia* s.s. and inhabit mostly low order montane tributaries. Sweeney (1978) has suggested that these low order tributaries that are too cool for *I. bicolor*, and that temperatures below 15°C growth and subsequent emergence are either reduced or not possible. It would appear that the species of the subgenus *Prionoides* originated in cool low order mountain streams. These species have however extended their ranges into the larger and warmer lower elevation streams (i.e *I. obscura*, *I. georgiae*) and have apparently succeeded by diapausing as an egg during the warmer summer months. Eggs begin to hatch apparently only after cooler seasonal fall temperatures return. Grant and Stewart (1980) observed a similar situation with *I. sicca* in Texas.

Isonychia obscura also occurred in abundance in the New River in Carroll County, Virginia (County Route 721) near the North Carolina border. The following data are summarized from Kennedy (1980). At this site the river width was about 150 m, with average depths of 0.5-2.5 m. The substrate was bedrock with overlying sand, gravel and rubble. _Podostemum ceratophyllum_ covered the substrate in riffle areas, mean flows averaged about 50 m3/s. Temperatures ranged from 0 C (February) to 25 C (August), dissolved oxygen ranged from 6.6 ppm (88%) to 9.4 ppm (125%). At this site _I. obscura_ was also univoltine, emerging in early and mid June. Nymphs were most commonly collected from mats of _Podostemum_, _Elodea_, and _Vallisneria_. Early instar nymphs were first collected in early September. _Isonychia bicolor_ also occurred in large numbers at this site.

Material:

Holotype M, North Carolina: Penrose, 7 July 1930, JRT (CU# 1086.1)

Georgia: Cherokee Co., Etowah River at junction of St. Rd S861, 6 1/2 mi. ESE of Ball Ground, 22-25 June 1971, W. L. Peters et al., 2 M, 18 N (FAMU); North Carolina: Haywood Co., Lake Junaluska, LB, 1 M (UF); Virginia: Carroll Co., New River, Co. Rt. 606, 15 June 1977, J. Kennedy, 1 M (reared) (VPI); same but 11-20 June 1980, BCK, 7 M, 7 F (reared) (VPI); same but 5-14 June 1981, 3 M, 2 F (reared) 7 N (VPI); Culpeper Co., Hazel River, off Co. Rt. 707, 3 July 1981, BCK, 1 M (reared), 4 F (VPI); Louisa Co., North Anna River, 100 yds upstream from bridge on St. Rt. 208, 25 June 1969, J. Marsh, 2 N (VPI); Montgomery Co., Little River, Co. Rt. 787, 13-24 June 1981, BCK, 3 M, 14 F (reared), 12 N (VPI).



Map 14. Distribution of I. obscura Traver.

Isonychia (*Prionoides*) *sayi* Burks

Isonychia sayi Burks, 1953: 110. Type locality: Rock Island, Illinois, M, F. Type deposition: (M) MCZ.

Baetis arida? Say, Walsh, 1862:370.

Baetis arida, Walsh (nec Say), 1863: 170; Walsh, 1863: 191.

Siphlurus aridus, Walsh (nec Say), Eaton, 1871: 129.

Chirotenetes aridus, Walsh (nec Say), Eaton, 1885: 206.

Isonychia arida, Walsh (nec Say), McDunnough, 1931: 159; Traver, 1935: 485.

Isonychia sp. A, Berner, 1950: 108.

Male Imago:

Body: length 9-14 mm, forewings 9-13 mm.

Head: Eyes purplish-gray with dorsal portion separated by lighter transverse bands; ocelli whitish; ocellar elevations dark purplish-brown. Antennae whitish to yellowish, tinged with brown. Sides of transverse shelf of face red brown, keel whitish.

Thorax: Mesonotum light brown; mesoscutellum and metanotum brown; pleura brownish. Prothoracic femur brown, apex dark brown, tarsal segments light brown; meo- and metathoracic legs whitish to light yellow. Wings hyaline with all veins whitish or light yellow, often with some veins light brown; forewings with whitish stain in stigmatic region, few crossveins anastomosed.

Abdomen: Terga 1-9 dark brown with light yellowish (sometimes diffuse) anterolateral spots (Fig. 24a); terga 1-9 with middorsal and submedian whitish to yellowish brown streaks or marks (Fig. 24b); tergum 10 yellow. Sterna 1-9 dark brown with yellowish anterolateral spots, becoming larger posteriorly; sterna 1-10 with 2-4 transverse whitish dots and usually with a pair of submedian streaks. sterna 2-9 with black dash just below pleural fold near each spiracle. Caudal filaments whitish to light yellow with no dark articulations. Forceps light brownish. Genitalia as Fig. 17.

Female Imago:

Body: length 10-15 mm, forewings 11-14 mm.

Head: Whitish to yellowish; ocelli whitish; ocellar elevations black; dorsally often with a pair of brownish diffuse stripes; posterolateral angles of occiput blackish; a blackish spot usually below compound eyes and between antennal scape. Antennae whitish tinged with brown.

Thorax: Mesonotum light brown; metanotum brown; pleura yellowish brown. Legs colored as male, often lighter. Wings hyaline with all veins dark brown or purple; forewings with whitish stain in stigmatic region.

Abdomen: Terga 1-9 dark brown with large yellowish anterolateral spots; terga 1-9 with middorsal and submedian yellowish (often diffuse) spots or streaks; tergum 10 yellowish. Sterna 1-10 brown with yellowish anterolateral spots; sterna 2-9 with a black dash below pleural fold near each spiracle. Caudal filaments whitish to light yellowish with no dark articulations. Subanal plate entire or slightly emarginate.

Egg: Typical of subgenus, however median region of knob-terminated coiled thread smaller in area, as compared with other species of Prionoides and the side without the knob-terminated coiled threads has a more distinctive pattern (Figs. 84-88).

Nymph:

Body: length 11-16 mm.

Head: Brown with whitish coronal stripe, sometimes forming a cross between compound eyes dorsally. Antennae whitish, scape and pedicel brownish basally, flagella with a brown transverse band about 1/2 distance from scape.

Thorax: Nota brownish with middorsal whitish stripe, very distinct on pronotum and mesonotum, usually forming a "Y" at base of mesonotum; small whitish spots and streaks anterior and lateral of mesothoracic wing pads. Legs brown with whitish markings, forefemora brown with whitish submedian and apical transverse bands, tibia whitish with median brownish transverse band, tarsi brown with basal whitish transverse band; tarsal claws with 7-11 marginal denticles. Procoxal gill as a tuft of multibranched light purplish or whitish filaments.

Abdomen: Terga brown; terga 1-9 with or without a middorsal stripe, sometimes with stripe only present on anterior portions of terga; color pattern of adult usually visible (yellowish anterolateral spots); terga 1-9 with whitish dots and streaks laterally and usually a brown spot at the posterolateral edge; tergum 10 whitish anteriorly, brownish posteriorly. Sterna variable, usually yellowish brown; lateral edges of sterna 1-9 with whitish and brownish maculae; adult color pattern visible. Gill lamella with large purplish median spot; median sclerotized streak brown; fibrillar portion whitish tinged with purple. Caudal filament brown, distally whitish.

Diagnosis:

Isonychia sayi is a very distinctive species within Prionoides. Male imagoes may be easily distinguished by the following combination of characters (1) veins hyaline or whitish, (2) caudal filaments whitish without dark articulations, (3) abdominal terga dark brown with light yellowish anterolateral spots, and (4) the distinctive penes. Females are similar to males except wing veination is brownish to purplish.

Nymphs were reared and associated for the first time from northwestern Florida by H. M. Savage and are separable from all other nymph of Prionoides by having coxal gills in tufts. They also apparently lack the two characteristic purplish-brown spots in the distal margin of the abdominal gill lamella.

Discussion:

This species has an interesting history as explained by Burks (1953). Dr. Burks renamed the species identified as *arida* Say by Walsh (1862) and subsequently by others *sayi*, after recognizing the true *arida*. *Isonychia sayi* with its *Siphlonurus* -like appearance and nymphs possessing coxal gill tufts is apparently not closely related to any other species of *Prionoides*. The penes usually have a small pair of membranous dorsoapical projections termed by McDunnough (1931) "apical tubercles." These are apparently not found on any other species of *Prionoides*.

Biology:

This species has been frequently collected by Dr. William L. Peters and co-workers from the Blackwater River near the Florida A & M University Biological Station in northwestern Florida. Beck (1973) and Peters and Jones (1973) have described the river. Summer water temperature maxima are near 30°C and winter minima are about 10°C (Peters and Peters 1977). *Isonychia sayi* nymphs (as *Isonychia* sp. A Berner

(1950)) were found by Peters and Jones (1973) to occur associated with bank vegetation and leaf litter. Berner (1950) reported that nymphs (as *Isonychia* sp. A) were found in flowing water where current was rapid. They were also frequently collected on well-anchored submerged logs, rocks and boards. Most frequently, however, they were collected among masses of debris and roots lodged in swift regions of sand bottomed streams. Berner states that apparently *I. sayi* may be captured throughout the year. Adults examined from Florida in this study were collected from April to June.

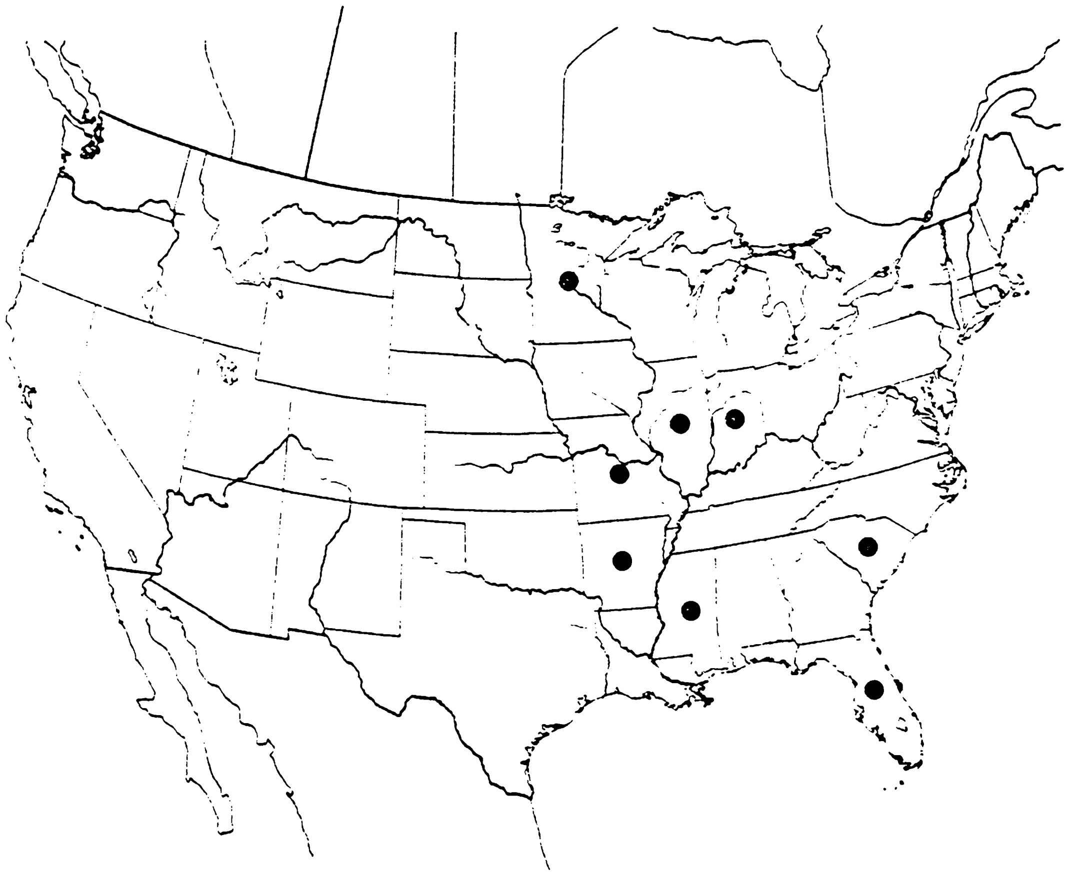
This species is rather rare in its northern range (McDunnough 1931). The male listed from Missouri has aberrant genitalia and the specimen is badly faded.

Material:

Holotype M, Illinois: Rock Island, 1863, B. D. Walsh, (31711) (MCZ); Allotype F, same (MCZ# 31711); Paratypes, same as Holotype, 1 M (MCZ), 2 F (INHS); Dixon, 27 June 1935, Delong and Ross, 1 M (INHS); Gulfport, Crystal Lake, 10 June 1939, J. S. Ayars, 1 M (INHS); Oquawka, 13 June 1932, H. L. Dozier, 2 F (INHS); Prophetstown, Rock River, 24-25 July 1947, Burks and Sanderson, 1 F (INHS); Rockford, at light, 29 June 1938, B. D. Burks, 1 F (INHS).

Arkansas: Black Rock, Black River, 22 May 1957, Ross and Stannard, 2 F (UU); Florida: Okaloosa Co., Blackwater River, Florida A & M Univ. Biol. Stn., 4 1/2 mi NW of Holt (at light), 14 April 1977, W. L. Peters et al., 3 F (FAMU); same but 16 April 1977, 5 M (FAMU); same but 21 April 1977, 1 M, 1 F (FAMU); same but 23 April 1977, 1 F (FAMU); same but 29 April, 1 M, 1 F (FAMU); same but 1 May 1978, 1 F (FAMU); Leon Co., Ochlockonee River, Ochlockonee Wildlife Mgmt. Area, 23 April 1981, H. M. Savage et al., 1 sub M, 5 sub F (reared), 6 M, 21 F, 3 N (VPI); Escambia River, Escambia River Survey #2, Stn. 4, 28 March 1953, SSR, 1N (ANSP); same but Stn 1, 30 March 1953, 5 N (ANSP); Illinois: C.V. Riley Coll., 1 M (USNM); Mississippi: Camp Shelby near Hattiesburg, 29 May 1944, C. D. Michener, 1 M (AMNH); Missouri: Roaring River State Park, June 1954, J. W. Green, 1 M (CAS); South Carolina: Aiken Co., Upper Three Runs Creek, about 0.1-1.0 mi upstream from SRP Road C and about 8 mi S of New Ellenton, 7 June 1972, J. W. Richardson, 1 N

(ANSP); S.R.P. # 4 Survey, Station 6B, 8 mi. above Allendale Bridge, 10 June 1952, SSR, 1 N (ANSP); Wisconsin: Dane Co., W. S. Marshall, 1 M (CNC).



Map 15. Distribution of I. sayi Burks.

Isonychia (Prionoides) serrata

Traver

Figs. 18a-b, 30, 89-91

Isonychia serrata Traver, 1932: 222. Type locality: Allen's Creek, Haywood County, North Carolina, M, F and nymph. Type deposition: (M) CU; Traver, 1935: 496.

Male Imago:

Body: length 15-16 mm, forewings 14-15 mm.

Head: Eyes rust brown to gray with dorsal portion separated by a darker transverse band; ocelli whitish or gray; ocellar elevations blackish purple usually with additional brownish tinting forming a dark triangular patch. Antennae purplish yellow, flagella segments purplish. Sides of transverse shelf purplish-brown. Remnants of maxillary palps purplish.

Thorax: Mesonotum yellowish brown, scutellum brown; metanotum purplish-brown; pleura brownish yellow. Prothoracic leg purplish-brown, basal half of femur and joint between femur and tibia yellowish purple, tarsi light brown to grayish purple, claws darker purple; meso- and metathoracic legs white, tarsal segments tinged with purple. Wings hyaline with all veins dark purplish-brown; forewings with purplish stain in stigmatic region, stigmatic crossveins anastomosed. Abdomen: Terga 1-9 yellowish brown, purplish-black bands on posterior margins, each band becoming diffusely purplish-brown anteriorly; terga 1-9 with yellowish brown middorsal stripe; terga 2-9 stripe bordered laterally by diffuse purplish-brown marks; terga 1-9 with posterolateral dark purplish brown triangular-like regions; tergum 10 yellowish; terga 2-9 with a black dash just below pleural fold near each spiracle. Sternum 1 brown with purplish tinting; sterna 2-4(5) purplish-brown with yellowish anterolateral regions; sterna 2-4(5) with 4 small median yellowish transverse dots; sterna 6-9 yellowish tinged and with purple with 2 median small yellowish transverse dots. Caudal filaments brown, distally slightly lighter, basal articulations light brown. Forceps light purplish-brown. Genitalia as Figs. 18a-b.

Female Imago:

Body: length 15-17 mm, forewings 14-16 mm.
Head: yellowish; ocelli grayish; ocellar elevations blackish purple. Antennae purplish yellow, flagella

purplish. Posteriolateral angles of occiput tinged with purple. Margins of transverse shelf of face shaded with reddish-brown and purple. Remnants of maxillary palps dark purple.

Thorax: Mesonotum yellow; metanotum yellowish tinged with purple. Pleura yellowish tinged with purple. Legs colored as male. Wings hyaline with all veins purplish-brown, anterior veins often reddish-brown; forewings with whitish stain in stigmatic area, some crossveins anastomosed.

Abdomen: Terga 1-10 yellowish with purplish-black bands on posterior margins; terga 1-10 with faint yellowish middorsal stripe, bordered laterally by purplish streaks; terga 1-6(7) posterior bands often diffusely purplish brown; terga 1-8(9) with posterolateral purplish-brown triangular-like regions; tergum 10 yellow. Sterna as male. Caudal filaments as male. Subanal plate usually with no posteromedian emargination.

Egg: Typical of subgenus (Figs. 89-91).

Nymph:

Body length 14-18 mm.

Head: Dark brown with whitish coronal stripe. Antennae whitish, scape and pedicel brown; flagella with brown transverse band 1/3 distance from scape; flagella often tinged with light brown.

Thorax: Nota dark brown with a middorsal whitish stripe. Pronotum with 2 pair of submedian crescentric marks; small whitish spots and streaks anterior and lateral of mesothoracic wing pads; mesonotum with a pair of whitish submedian spots. Legs dark brown with whitish or yellowish marking, forefemora dark brown with whitish to yellowish submedian and apical transverse bands, sometimes a obscure basal transverse band; tibia yellowish with median brownish transverse band, tarsi yellowish with submedian brownish transverse band; tarsal claws with 5-11 marginal denticles. Procoxal gill a single robust purplish filament.

Abdomen: Terga dark brown; terga 1-9 with a wide middorsal yellowish or whitish stripe, occasionally stripe faint on middle segments. Color pattern of adult faintly visible. terga 1-9 with a pair of submedian crescent-like light streak bordering middorsal stripe, these streaks sometimes bordered thinly with black;

terga 1-9 with an obscure whitish dot near anterolateral edge; tergum 10 yellowish anteriorly, brown posteriorly. Sterna brown; sterna 1-9 with a yellowish anterior midventral spot, a pair of yellowish submedian crescentric bars and four transverse dots; sterna 1-9 with a black obscure spot near lateral edges. Gill lamella purplish, two brownish purple spots in distal margin; median sclerotized streak brown; fibrillar portion purplish. Caudal filaments brown, distally whitish, blacklish at tips, middle filaments sometimes lighter.

Diagnosis:

This species may be distinguished by the following combination of characters: (1) incurved dorsomedial flap saw-like with 6-9 teeth, (2) lacking distinct submedian oblique or concentric lateral marks on terga 1-9, and (3) caudal filaments brown, lighter at extreme tips with no darker articulations. The nymph is very similar to I. similis and I. notata, but can be usually identified by possessing a wide pale middorsal stripe on terga 1-9. It is also usually more uniformly darker than the preceeding species.

Discussion:

As typical with the subgenus _Prionoides_, the penes are variable. Occassionally the diagnostic saw-like flap of 6-9 teeth is more apparent only on one side with the other having less than 6 teeth. The medial swelling of the holotype as depicted by Traver (Fig. 18) is apparently an artifact of mounting or of the original teneral condition of the specimen.

Biology:

This rather large species emerged late as compared to the other species of _Prionoides_. Most records are from July to September. A large population occurs in Fox Creek located in Grayson County, Virginia (County Route 603). This excellent trout stream is located in the Blue Ridge Physiographic Province of Virginia, draining part of the highest peak in Virginia (Mount Rogers, 1746 m). The median width of the stream at the collection site was 2m. Substrate consisted of pebble (16-64mm) and cobble (64-128mm) overlying bedrock. PH averaged 7.2 and alkalinity 11 mg/l $CaCO_3$. Early instar nymphs were first collected in late May and adults emerged from mid-July to August. There, was apparently only one generation per year.

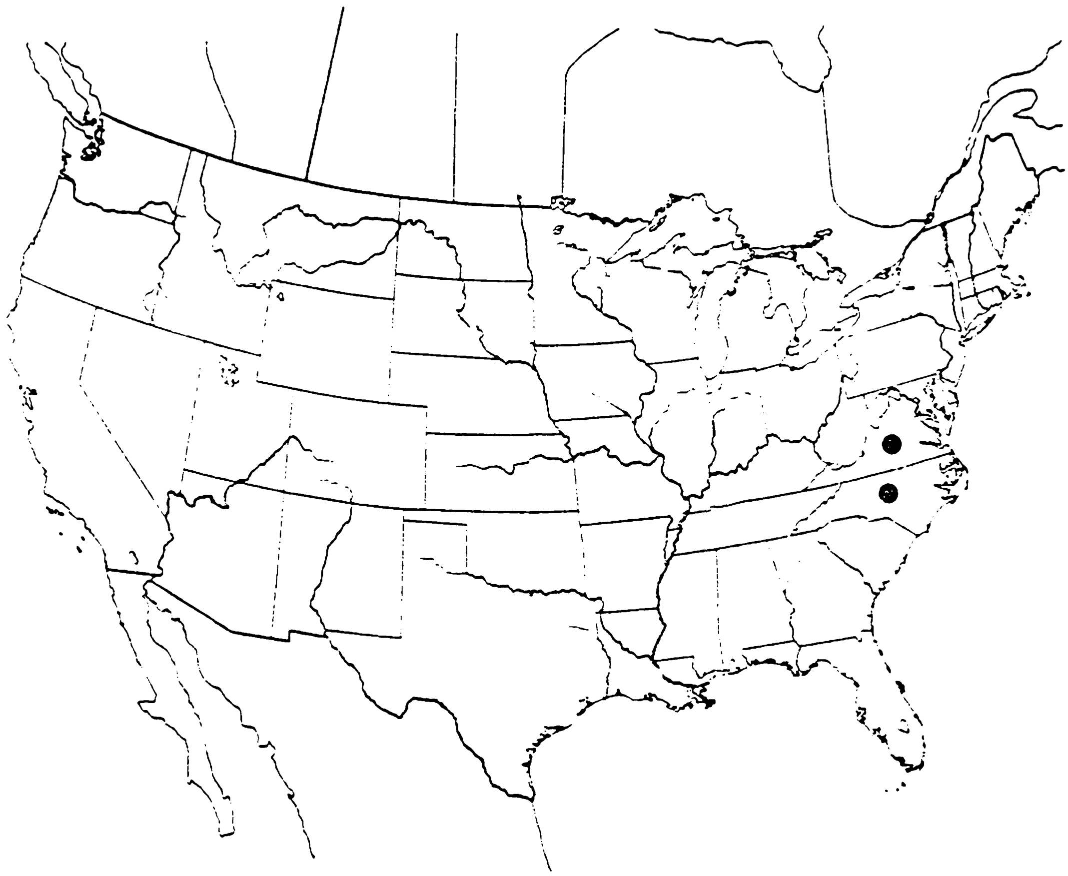
The type locality of *I. serrata* was visited in early July 1981. Allen Creek has undergone much perturbation recently by the expansion of the city of Waynesville, including construction of a large dam for the Waynesville Watershed Project. This species was not recollected from Allen Creek proper, but from a small tributary, Rocky Branch (County Route 1219) just below the dam. There immature nymphs were most commonly collected under large flat rocks and ledges and debris. Water temperature at time of collection was 15 C.

Material:

Holotype M, North Carolina: Tributary of Pigeon River, Waynesville, 21 July 1930, JRT (CU# 1085.1); Allotype F, Allen's Creek, Hazelwood, 23 July 1929, JRT (CU# 1085.2).

North Carolina: Tributary of Pigeon River, 15 July 1929, JRT, 4 N (CU); Allen's Creek, 18 July 1929, JRT, 1 N (CU); Haywood Co., Rocky Branch of Allen's Creek, Co. Rt. 1219, 7 July 1981, BCK, 10 N; Yancey Co., Bald Creek, St. Rt. 19 near Wallow Creek confluence, 9 July

1981, BCK, 4 M, 8 F (reared), 8 L; Virginia: Grayson Co., Fox Creek, Co. Rt. 603, 18 July 1981, BCK, 2 N; same but 30-31 July 1981, 3 M, 11 F (reared), 12 N (VPI).



Map 16. Distribution of *I. serrata* Traver.

Isonychia (*Prionoides*) *similis*

Traver

Figs. 19a-b, 21, 92-95

Isonychia similis Traver, 1932: 213. Type locality: Cedar Creek, Jackson County, North Carolina, M, F and nymph. Type deposition: (F) CU; Traver, 1935: 498.

Isonychia aurea Traver, 1932: 224. Type locality: Small tributary (Plott Creek?), Haywood County, North Carolina, F and nymph. Type deposition: (F) CU; Traver, 1935: 486. New Synonymy

Male Imago:

Body: length 12-16 mm, forewings 12-15 mm.
Head: Eyes rust brown to gray with dorsal portion separated by a lighter transverse band; ocelli whitish or grayish; ocellar elevations blackish purple. Antennae whitish or light brown, flagella tinged with purple. Sides of transverse shelf light orangish to light brown, edges margined with purplish brown. Remnants of maxillary palps purplish.
Thorax: Mesonotum yellowish brown; metanotum brown. Pleura yellowish with membranes often purplish. Prothoracic leg purplish-brown, femur basally light

yellowish purple; meso- and metathoracic legs whitish to yellowish, tarsi tinged with purple. Wings hyaline with all veins purplish-brown; forewings with brownish stain in stigmatic region, stigmatic crossveins anastomosed.

Abdomen: Terga 1-9 yellowish-brown, wide purplish-brown bands on posterior margins, each band becoming diffusely light purplish-brown anteriorly; terga 1-9 with a yellowish brown middorsal stripe, sometimes stripe not discernable from background color; terga 2-9 middorsal stripe bordered laterally by purplish-brown streaks, streaks often diffuse and crescentric-like on terga 8-9; terga 2-9 with faint lateral streaks; terga 1-9 posteriolateal angles purplish-brown; tergum 10 yellowish orange. Black dash below pleural fold near each spiracle. Sterna 1-9 light yellowish orange to purplish-brown; sterna 2-3(4) with 2 pairs of transverse light dots. Caudal filaments brown, distally becoming lighter, this distal portion marked with darker brown articulations. Forceps light yellowish brown. Genitalia as Figs. 19a-b.

Female Imago:

Body: length 15-16 mm, forewings 14-15 mm.

Head: Yellowish; ocelli grayish; ocellar elevations blackish purple. Antennae brown tinged with purple. Posterolateral angles of occiput purplish; edges of transverse shelf shaded with reddish and tinged with purple. Remnants of maxillary palps purple.

Thorax: Mesonotum yellow; metanotum light yellowish brown tinged with purplish brown. Legs colored as male. Wings hyaline, with all veins purplish-brown, stigmatic region with brown stain, stigmatic crossveins anastomosed.

Abdomen: Terga 1-10 yellowish orange with purplish-brown bands on posterior margins interrupted medially by a faint yellowish brown middorsal stripe; terga 2-9 middorsal stripe bordered laterally by purplish-brown streaks, streaks larger on terga 2-5; terga 2-9 with lateral streaks faint; terga 1-9 posterolateral angles purplish-brown; tergum 10 yellowish. Black dash below pleural fold near spiracles. Sterna as male. Caudal filaments as male. Subanal plate with very shallow emargination.

Egg: Typical for subgenus (Figs. 92-95).

Nymph:

Body: length 11-16 mm.

Head: Brown with whitish often obscure coronal stripe. Antennae whitish to yellowish, scape and pedicel brownish, flagella usually with a light brown transverse band 1/3 distance from scape, occasionally band faint or absent.

Thorax: Nota brown usually with a faint whitish middorsal stripe, more distinct on pronotum and anterior portion of mesonotum; pronotum usually with 2 pairs of submedian spots or crescentric marks; small whitish spots or streaks anterior and lateral of mesothoracic wing pads; a pair of median whitish spots on mesonotum. Legs brown with whitish or yellowish markings, forefemora brown with yellowish basal, submedian and apical transverse bands, bands sometimes obscure, tibia whitish or yellowish wwith median brownish transverse band, tarsi yellowish with a submedian or basal brown band; tarsal claws with 5-11 marginal denticles. Procoxal gill a single robust purplish filament.

Abdomen: terga brown; terga 1(2)-9 either with a middorsal whitish or yellowish orange streak or blotch or terga 1-5(6) with a whitish middorsal thin stripe on anteriorly. Color pattern of adult faintly visible (purplish streaks or blotches bordering middorsal stripe); terga 1-9 with a pair of submedian crescentric-like light streaks bordering stripe; terga 1-9 with a whitish spot near lateral edge; tergum 10 yellowish brown. Sterna brown; sterna 1-9 with a pair of midventral crescentric bars and 2 pairs of light transverse dots, outer pair often fused with posterior end of bars; sterna 1-9 with a blackish spot near lateral edge. Gill lamella purplish; two brownish spots distal margin; median sclerotized streak brown; fibrillar portion purplish. Caudal filaments brown to yllowish orange, distally whitish, tips blackish.

Diagnosis:

Males of *Isonychia similis* may be distinguished by the following combination of characters: (1) penes with anterolateral angles rounded and (2) caudal filaments brown basally, lighter distally with distal portion marked with darker brown articulations. The nymph is apparently similar to *I. notata* and can be separated by the larger number of stout spines on the foretibia.

Discussion:

Isonychia similis was originally described from two female imagoes and one male imago, a female designated the holotype. The single male had its subimago exuviae artifically removed (Traver 1932).

Isonychia aurea was originally described from only two female imagoes and one female subimago. I collected and reared male imagoes from the probable type locality stream of *I. aurea* (Plott Creek) near Hazelwood, North Carolina. The male genitalia were of the same unique type as *I. similis* and color and maculation were within limits of variation typically encountered in *Prionoides*. I also examined additional male imagoes reared by Dr. Berner from Macon County, North Carolina. Based on all of the above I place *I. aurea* as a junior synonym of *I. similis*.

I also visited the type locality stream of *I. similis*, Cedar Creek (Jackson County, North Carolina, County Route 1120). This stream has undergone several severe alterations. Much of the lower portion of the creek was inundated by Torpe Reservoir and the upper portion is under the influence of a small private dam and lake. Only a few nymphs were collected after considerable effort and none were successfully reared.

Biology:

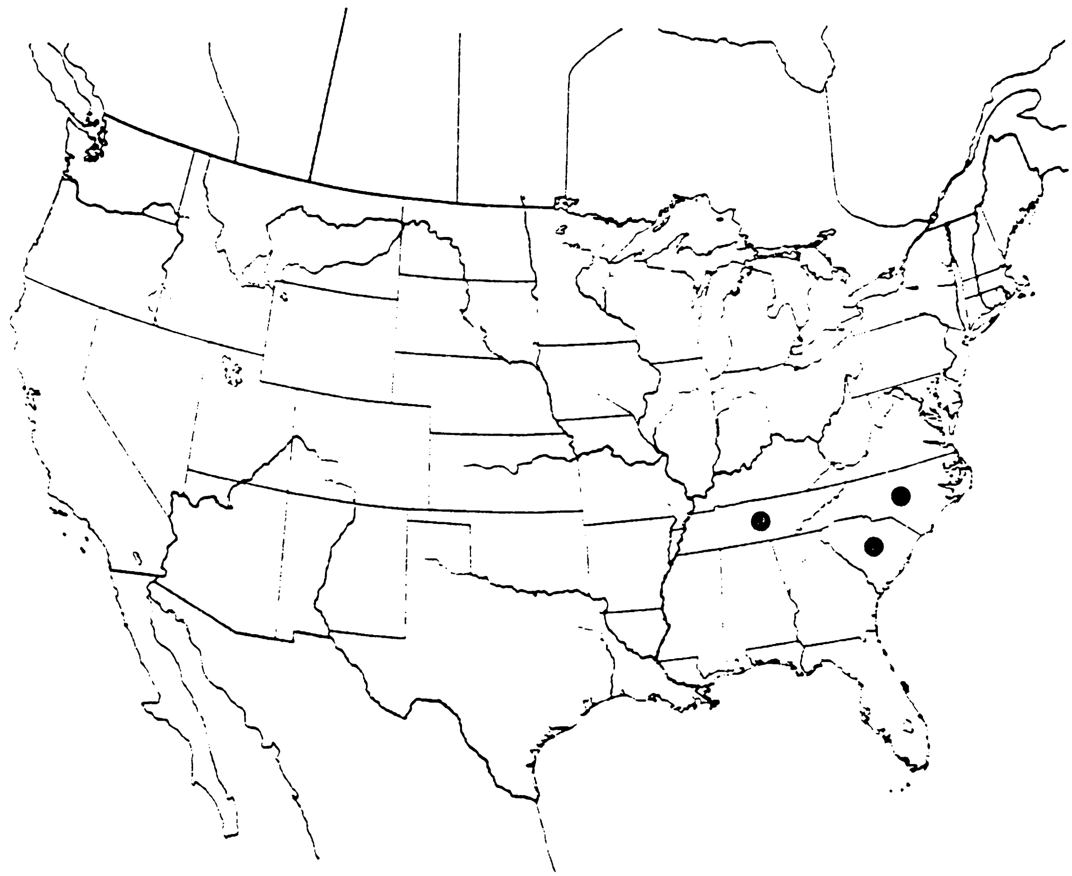
This species along with *I. serrata*, emerge late in the season from July to September. Nymphs have been collected in cool 3rd and 4th order Appalachian streams. The water temperature at the time of the Plott Creek collections (7 July) was 16°C and at Cedar Creek (17 July) 18°C.

Material:

Holotype F, *Isonychia similis*, North Carolina: Cedar Creek, 29 July 1930, JRT (CU# 1092.1); Allotype M, same but 24 July 1930 (CU# 1092.2); Paratype F, same but 29 July 1930 (CU# 1092.3); Holotype F, *Isonychia aurea*, North Carolina: Tributary of Pigeon River, Hazelwood, 26 July 1930, JRT (CU# 1090.1); Allotype F, same but 25 July 1929 (CU# 1090.2); Paratype F, same but 22 July 1929 (CU# 1090.3).

North Carolina: Haywood Co., Plott Creek, end of Co. Rt. 1173, 7 July 1981, BCK, 2 M (reared), 12 L (VPI); Jackson Co., Cedar Creek, Co. Rt. 1120, 9 July 1981, BCK, 3 N (VPI); Macon Co., Big Creek (Bad Branch) 17 Aug 1948, LB, 2 M (reared) (UF); South Carolina: Sumter

National Park, 12 July 1957, LB, 1 M (UF); Tennessee: Greene Co., Cummins Branch into Paint Creek, 11 Sept 1981, BCK, 1 M (reared) 2 F (VPI).



Map 17. Distribution of _I. similis_ Traver.

Since females and nymphs of the subgenus Prionoides are difficult to identify specifically and because of the possibility of several undescribed species the following records are being listed to augment distributional information and stimulate further collecting from these localities:

Florida: Escambia River, Escambia River Survey # 2, Station 1, 30 Mar 1953, S. S. Roback, 1 N (ANSP); Georgia: Rabun Co. Coleman River at junction with Tallulah, 15 July 1969, J. B. Wallace and F. F. Sherberger, 1 N (CL); Maine: Penoboscot Co., Penoboscot River, Winn, 17 Jun 1980, T. M. Mingo, 1 N (TM); University of Maine Campus, at Light, 25 July 1979, T. M. Mingo, 1 F (TM); Washington Co., Narraguagus River, Site 4, 6 Jul 1973, T. M. Mingo, 16 N (TM); Pennsylvania: Chester, Devon at light, 7 July 1964, S. S. Roback, 1 F (ANSP). South Carolina: Aiken Co., Upper Three Runs Creek, ca. 0.1-1.0 mi. upstream from SRP Road C and ca. 8 mi. S of New Ellenton, 6 June 1972, J. W. Richardson, 2 F (ANSP); Clemson, Farm pond (sic) 13 Sept 1967, M. J. Barrisi, 2 N (CL);

PHYLOGENY

Edmunds (1975) has hypothesized that one lineage of the siphlonurids (possessing most ancestral ephemeropteran character states), a Isonychia -like ancestor gave rise to the derived Oligoneuriidae and evolved on Gondwanaland before the Cretaceous, later spreading into temperate regions of Laurasia. Fossils are apparently known from the Miocene (Edmunds 1975) and Oligocene (Lewis 1977). However, the phyletic origin of the Isonychiinae (sensu McCafferty and Edmunds 1979) relative to the Oligoneuriidae and Siphlonuridae is very unclear and has been subject to several recent interpretations (Edmunds 1972, Edmunds 1973, Riek 1973, Edmunds 1975, McCafferty and Edmunds 1979).

Today the genus Isonychia is apparently primarily Holarctic with a few Oriental and Neotropical species. The Oligoneuriidae on the otherhand, are apparently primarily Amphinotic, Ethiopian, Oriental, and Neotropical, with only several Holarctic species. The widespread Holarctic distribution may indicate that Isonychia is very old when compared to other mayfly taxa that have no connections among the southern continents except via Laurasia.

My hypothesis for the distribution of the Holarctic Isonychia is based on the acceptance of two suppositions, (1) the subgenus Prionoides is the link with the Siphlonurid ancestor (prehaps a Cronicus -like mayfly) and the more derived Isonychia s.s, possessing such primitive traits as the subgenital plate with broad or a slight posteromedian inmargination, penes armed dorsally with stout serrations or spines, and in general inhabiting smaller and cooler streams, and (2) the species of Isonychia occurring today in the Oriental and Neotropical realms are of relative recent invasions.

Therefore, the North American biogeography of the genus may have included one or more of the following events: (1) invasion of North America via the "asiamerican" land mass of the Cretaceous by a Gondwanian Isonychia and subsequent latter reinvasion of Eurasia in the Tertiary by the extant genus Isonychia via land routes across the North Atlantic (Cutt and Laving 1977). This version may have also included a latter invasion of a Eurasian lineage of

Isonychia (_ignota_ group) via the Beringian connection in the Pliocene-Pleistocene. _Isonychia_ _velma_ may be such a relict.

(2) Another version might have included a divergence of _Isonychia_ into distinct lineages now prehaps represented by the two subgenera already on the North American-Eurasian land mass of the late Jurassic or Cretaceous and latter extinction of the _Prionoides_ lineage in Eurasia. The very incomplete knowledge of the Palearctic and Oriental forms precludes any further speculation on this hypothesis.

The early _Isonychia_ mayflies may have been adapted to lower order cool streams of higher elevations of the sedimentary Appalachians of eastern north America. These mayflies were probably like or very similar to the subgenus _Prionoides_. As the boreotropical realm gradually cooled _Isonychia_ may have slowly dispersed and split into the _Isonychia_ s.s lineage, colonizing warmer and lower elevational habitats. The climatic fluctuations of the Quaternary glaciations may have been responsible for some of the distributional patterns of observed today. The ice-free areas of the southern Appalachians provided refugia and allowed

Isonychia to revade northern and more western regions. However, this reinvasion may not been entirely successful because of some inability to develop in very cold water temperatures. *Isonychia* is absent or poorly represented in the Arctic, Hudsonian, and Canadian faunal areas (Allen 1892) of North America. *Isonychia* s.s. generally appears to be a warm water adapted group. Also the subgenus *Prionoides* is apparently primarily southern Applachian in distribution with only a very few poorly known species as far north as Maine.

Isonychia s.s was successful (especially the *sicca* group) in dispersing and colonizing the upper and lower austral zones (Merriam 1892) adapting to warm and often sandy low gradient streams. *Isonychia* is conspicuously absent or poorly represented in the Rocky Mountains perhaps further substantiating a much older eastern connection via the North Atlantic routes than rather a more recent Beringian connection.

The invasion into Mesoamerica via the Mexican Transition Zone is probably Pliocene-Pleistocene, originating from eastern Texas populations.

The nymphs and adults of *Isonychia* are morphologically homogenous and provide few reliable

Character States Used in Fig. 6a

Character	Primitive	Advanced
Egg:		
1. Egg shape	biconvex	spherical
Nymph:		
2. Apical margin of gill lamella	without spines	with spines
3. Procoxal gill	single filament	multibranched filaments
Adult:		
4. Posteromedian emargination of subgenital plate	slight or absent	deep
5. Penes with incurved dorsal flap aimed with serrations and spines	present	absent
6. Emargination of subanal plate	slight	deep
7. Penes dorsal lobes	with flap on medial edge	without flap
8. Color of forelegs	entirely brown	bicolor
9. Posterolateral margins of dorsal penes lobes	rounded, with base and distinct constriction	broadly rounded or subtruncate, but without a distal constriction

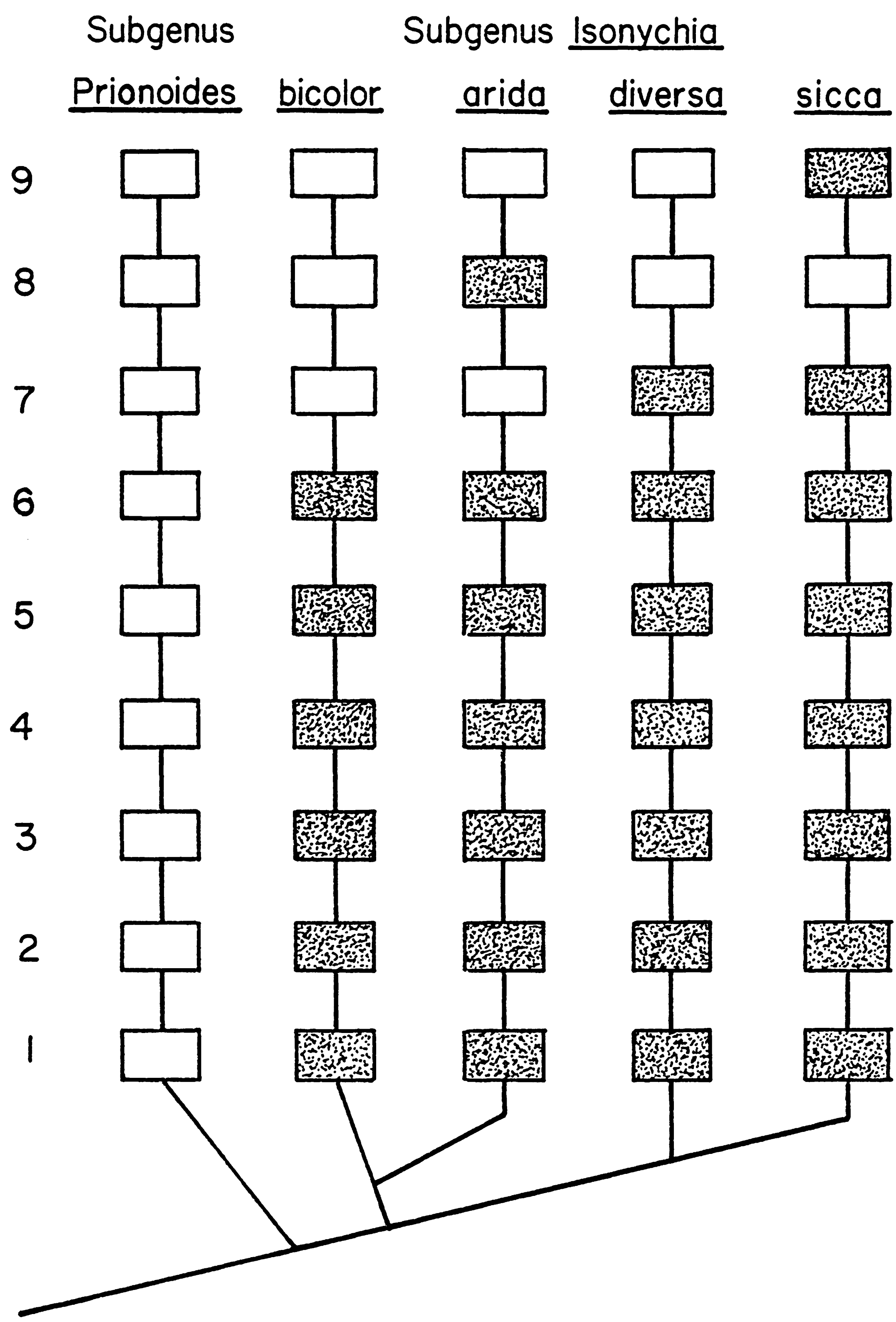


Fig. 6a. Proposed phylogeny of North American Isonychia.

phyletic characters. The presence of monoapomorphies rather than synapomorphies prevents a thorough cladistic analysis (Table 5).

The evolution of the Nearctic Isonychia is outlined in Fig. 5a.

In the subgenus Prionoides, I. distincta, I. georgiae, I. notata, I. obscura, I. similis, and I. serrata, form a group of very closely related species probably having a common ancestor. They generally inhabit lower order cool and clear streams of the Applachians and upper Piedmont. The remaining species of this subgenus, I. sayi, is apparently distantly related to the previous cluster. It is rather widespread in distribution with apparently wide ecological tolerances. The phyletic relationship between these two groups is unknown,

In the subgenus Isonychia, 4 species clusters are evident on the basis of male genitalia. Cluster I, th bicolor group and cluster II, the arida group form two closely related lineages. Both possess penes with dorsal lobes with a prominent flap on the medial edge. Both groups probably shared a similar ancestor.

Cluster III includes 5 very closely related species, _I. berneri_, _I. campestris_, _I. edmundsi_, _I. intermedia_, and _I. sicca_, sharing a common ancestor. They all usually inhabit warmer and often higher order sandy streams. _Isonychia camprestris_ the most northern distributed species of this cluster, most likely represents a population derived from a more southern population of _I. sicca_ adapted to the more northern plains and boreal forest.

The relative origin and phyletic relationship of the _I. diversa_ group to the _sicca group_ cannot be ascertained at this time because of the incomplete knowledge of the latter species.

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APPENDIX

Figures 1 a-h. Male genitalia, dorsal. *I.* (*Isonychia*) *bicolor*. a, Holotype of *I. albomanicata*; b, Holotype of *I. christina*; c, Holotype of *I. circe*; d, Holotype of *I. fattigi*; e, Holotype of *I. harperi*; f, Holotype of *I. matilda*; g, Holotype of *I. pacoleta*; h, Holotype of *I. sadleri*.

Figures 2-4 and 7. Male genitalia, dorsal, *Isonychia* s.s., 2, *I. rufa*; 3, *I. tusculanensis*; 4, *I. velma*; 5, *I.* (*Isonychia*) subanal plate; 6, *I. arida*.

Figure 7. foreleg of *I. arida*. Figures 8-13. Male genitalia, dorsal. *I.* (*Isonychia*). 8, *I. berneri*; 9, *I. campestris*; 10, *I. edmundsi*; 11, *I. intermedia*; 12a-b, *I. sicca*, a, Texas, b, Texas and Illinois; 13, *I. diversa*.

Figures 14-15. Male genitalia, dorsal. *I.* (*Prionoides*). 14, *I. distincta*; 15a-g, *I. georgiae*; a, Holotype; b, Holotype of *I. thalia*; c, Town Creek, GA; d, Davidson River, NC; e, Holotype *I. annulata*; f, Big Alamance Creek, NC; g, Cullasaja River, NC.

Figures 16-18a. Male genitalia, dorsal. I. (Prionoides). 16a-e, I. obscura; a, Holotype; b, New River, VA; c, Ball State Park, GA; d, Hazel River, VA; e, Little River, VA; 17, I. sayi; 18a, Holotype of I. serrata.

Figures 18b-19. Male genitalia, dorsal. I. (Prionoides). 18b, I. serrata, Fox Creek; 19a-b, I. similis; a, Allotype of I. similis; b, Big Creek, NC; 20-22, subanal plates; 20, I. georgiae; 21, Holotype of I. aurea; 22, Holotype of I. notata.

Figures 23-28. Adult abdomens. 23a-b, I. (Prionoides) distincta, a, lateral, b, dorsal; 24a-b, I. (Prionoides) sayi, a, ventral, b, dorsal; 25, I. (Isonychia) bicolor, lateral; 26, I. (Isonychia) velma, lateral; 27, I. (Isonychia) edmundsi, lateral; 28, I. (Isonychia) intermedia, lateral.

Figures 29-33. Wings. 29, I. (Isonychia) bicolor; 30, I. (Prionoides) serrata; 31, I. (Isonychia) tusculanensis; 32, I. (Isonychia) velma; 33, I. (Isonychia) edmundsi.

Figure 34. Mouthparts of Isonychia velma, abbreviations of terminology: Lm (labrum), Md (mandibles), Mx (maxillae without gill filaments), lb (labium), Hphy (hypopharynx), Lin (lingua), Slin (superlingua).

Figures 35-40. 35, nymphal foreleg, _I_. (_Prionoides_) _obscura_; 36-37, ventral apical cleft of mesothoracic femur; 36, _I_. (_Isonychia_) _bicolor_; 37, _I_. (_Isonychia_) _rufa_; 38, nymphal thorax, dorsal, _I_. (_Isonychia_) _intermedia_; 39-40, leading dorsoapical edge of nymphal prothoracic femur; 39, _I_. (_Isonychia_) _intermedia_; 40, _I_. (_Isonychia_) _sicca_.

Figures 41-43, nymphal terga 7-9, 41-42, _I_. (_Isonychia_) _bicolor_, 43, _I_. (_Isonychia_) _tusculanensis_; 44-45, nymphal sterna 7, 44a-b, _I_. (_Prionoides_) _georgiae_; 45, _I_. (_Prionoides_) _obscura_; 46-47, 7th nymphal gill, 46, _I_. (_Isonychia_); 47, _I_. (_Prionoides_).

Figures 48-51. _I_. (_Isonychia_) _bicolor_, eggs. 48, Big Alamance Creek, NC, 500X; 49, same, details of knob-terminated coiled threads, 5000X; 50, Rapidan River, VA, 500X; 51, from _matilda_ type imago, 375X.

Figures 52-55. _I_. (_Isonychia_), eggs. 52, paratype of _sadleri_, 500X; 53, _I_. _rufa_, IN, 500X; 54 _I_. _tusculanensis_, VA, 500X; 55, _I_. _velma_, CA

Figures 56-59. _I_. (_Isonychia_), eggs, 56, _I_. _velmae_, details of knobterminated coiled threads, 1000X; 57, _I_. _arida_, FL, 500X; 58, *I. arida*, SC, 500X; 59, *I. arida*, details of knob-terminated coiled threads, 2000X.

Figures 60-63. *I.* (*Isonychia*), eggs, 60, *I. berneri*, 500X; 61, same, 500X; 62, *I. campestris*, Sask., 500X; 63, same, 500X.

Figures 64-67. *I.* (*Isonychia*), eggs, 64, *I. edmundsi*, Honduras, 500X; 65, same, 500X; 66, *I. intermedia*, NM, 500X; 67, same, 500X.

Figures 68-71. *I.* (*Isonychia*), eggs, 68, *I. intermedia*, details of knob-terminated coiled threads, 1000X; 69, *I. intermedia*, details of knob-terminated coiled threads, 5000X; 70, *I. sicca*, TX, 500X; 71, *I. sicca*, IL, 500X.

Figures 72-75. *I.* (*Prionoides*), eggs. 72, lateral, illustrating ridge, 350X; 73, *I. distincta*, 310X; 74, same, details of chorion; 520X; 75, *I. georgiae*, allotype of *I. thalia*, 310X.

Figures 76-79. *I.* (*Prionoides*), eggs. 76, *I. georgiae*, Davidson River, NC, 280X; 77, *I. georgiae*, allotype of *I. annulata*, 210X; 78, *I. georgiae*, side without knob-terminated coiled threads, 310X; 79, *I. georgiae*, Towns Creek, GA, 270X.

Figures 80-83. _I_. (_Prionoides_), eggs. 80, _I_. _georgiae_, details of knob-terminated coiled threads, Davidson River, NC, 5000X; 81, Holotype of _I_. _notata_, 200X; 82, same, details of chorion, 500X; 83, _I_. _obscura_, VA, 285X.

Figures 84-87. _I_. (_Prionoides_), eggs. 84-87, _I_. _sayi_, FL, 84, 350X; 85, details of knob-terminated coiled threads, 5000X; 86, side with knob-terminated coiled threads, 210X; 87, details of chorion of side with knob-terminated coiled threads, 2000X.

Figures 88-91. _I_. (_Prionoides_), eggs. 88, _I_. _sayi_, details of micropylar device; 89, Allotype of _I_. _serrata_, 210X; 90, same, details of chorion, 550X; 91, _I_. _serrata_, side without knob-terminated coiled threads, Fox Creek,VA, 225X.

Figures 92-95. _I_. (_Prionoides_), eggs. 92, Holotype of _I_. _similis_, 210X; 93, same, details of chorion, 550X; 94, Holotype of _I_. _aurea_, details of chorion , 550X; 95, same, side without knob-terminated coiled threads, 550X.

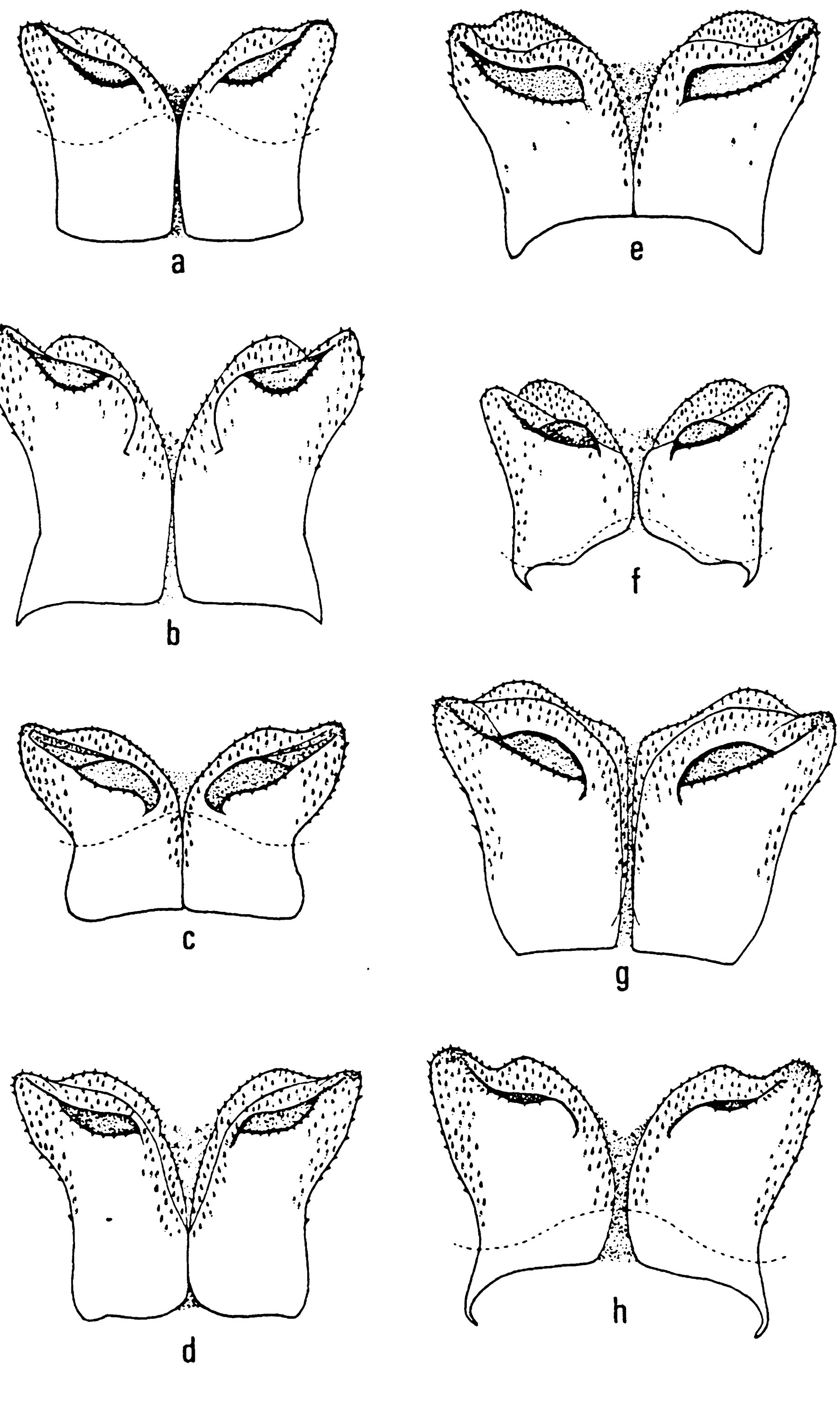
Figures 96-99. _I_. (_Isonychia_) _bicolor_, male genitalia, dorsal, 96, 250X; 97, 310X; 98, 560X; 99, illustrating sperm extrusion, 200X.

Figures 100-101. _I_. (_Isonychia_) _rufa_, male genitalia dorsal, 100, 200X; 101, 310X; 102, nymphal mouthparts, frontal, _I_. (_Prionoides_) _obscura_, 55X; 103, Nymphal forecoxal gill, _I_. (_Prionoides_) _georgiae_, 200X.

Figures 104-105, _I_. (_Isonychia_) _bicolor_, nymphal forecoxal gill tuft, 200X; 105, same, 200X; 106, Distal edge of anterior margin of nymphal abdominal gill 7, _I_. (_Isonychia_) _sicca_, 200X; 107, Median sclerotized ridge of nymphal abdominal gill 7, _I_. (_Isonychia_) _sicca_, 500X.

Figures 108-110, Nymphal abdominal gill 7, 108, Distal edge of anterior margin, _I_. (_Isonychia_) _bicolor_, 200X; 109, apical margin, _I_. (_Isonychia_) _bicolor_, 500X; 110, apical margin, _I_. (_Prionoides_), 70X; 111, Posterior margin of 6th tergum, _I_. (_Prionoides_), 500X.

Figure 112, Nymphal outer nymphal caudal filament, _I_. (_Prionoides_), 500X; 113, _Cocconeis_ _placentula_, on nymphal abdominal gill surface, 5000X.



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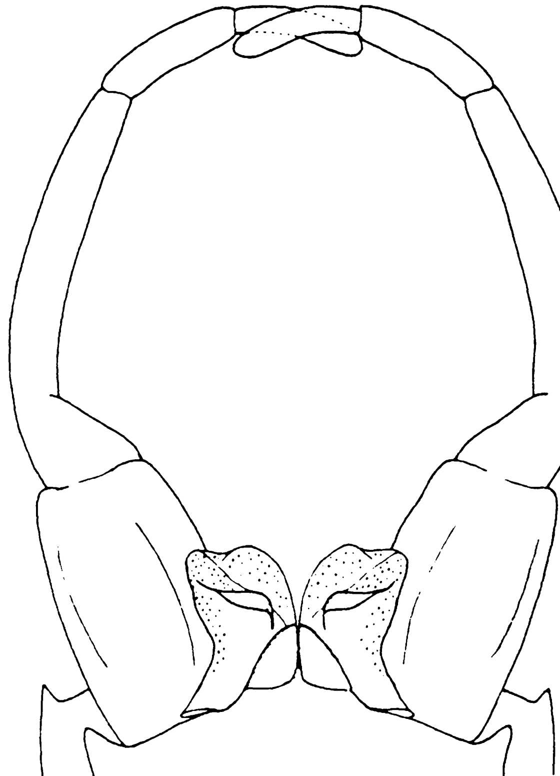

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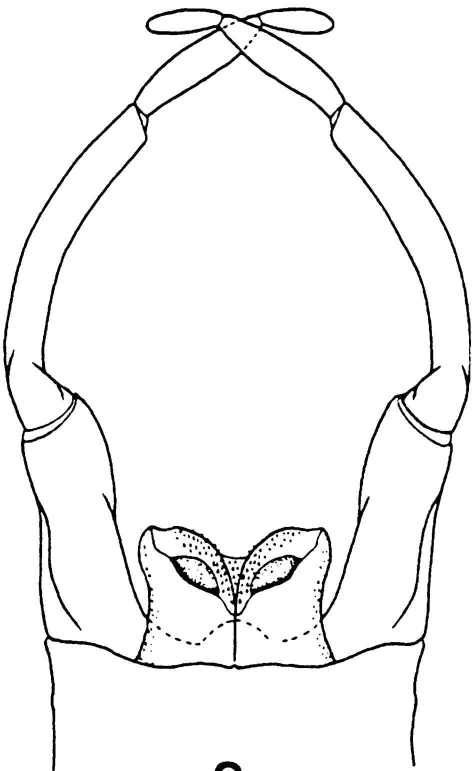

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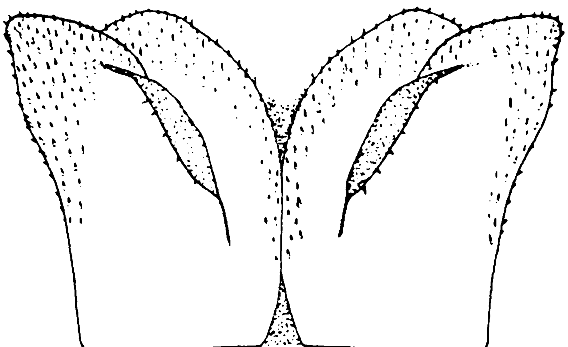

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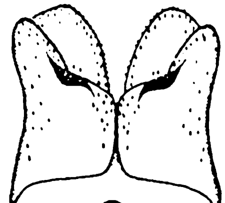

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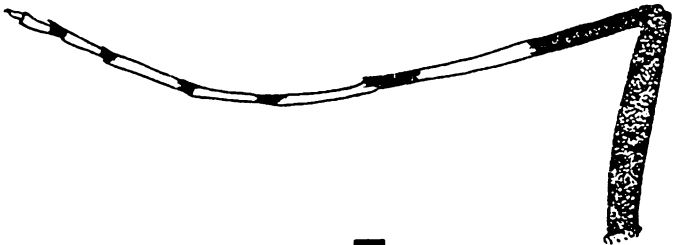

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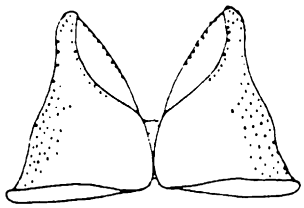

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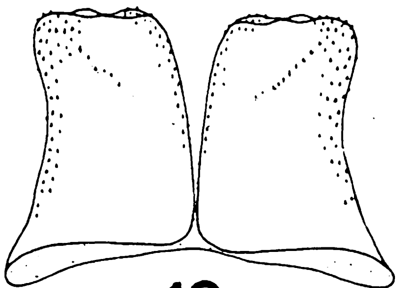

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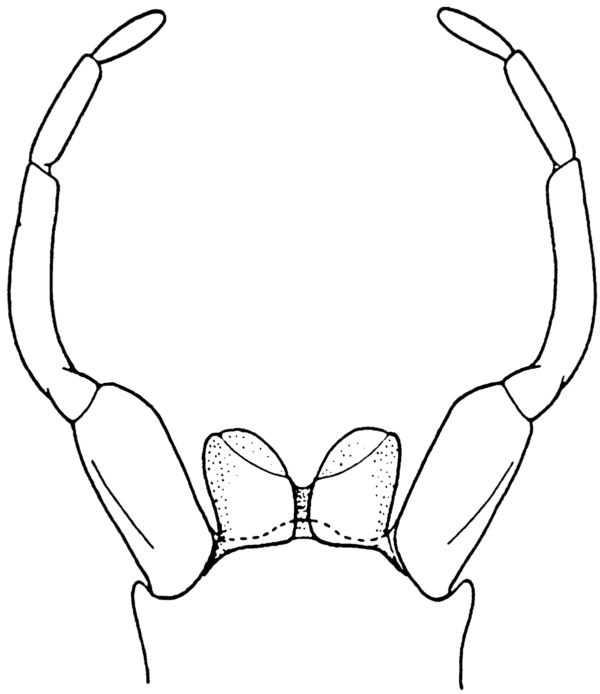

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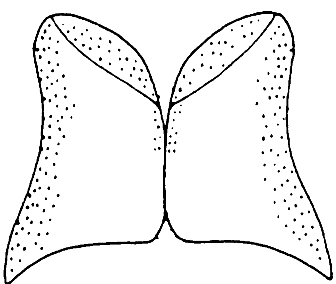

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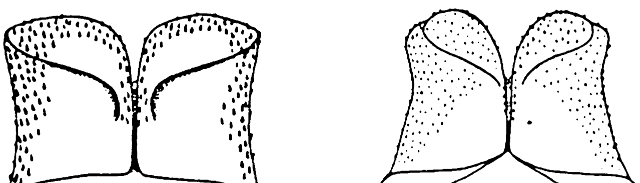

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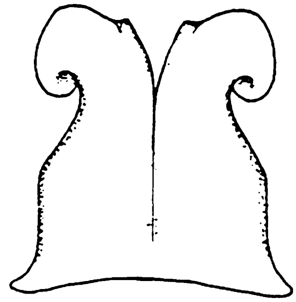

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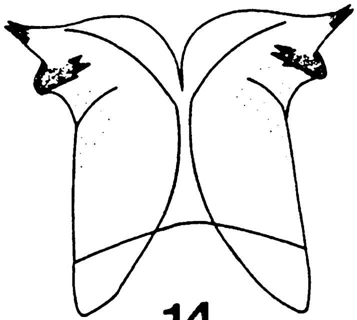

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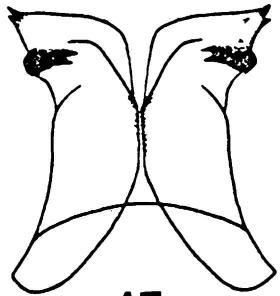

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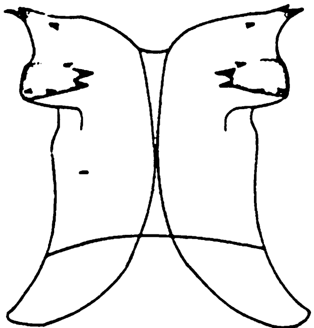

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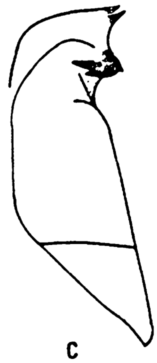

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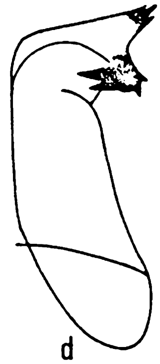

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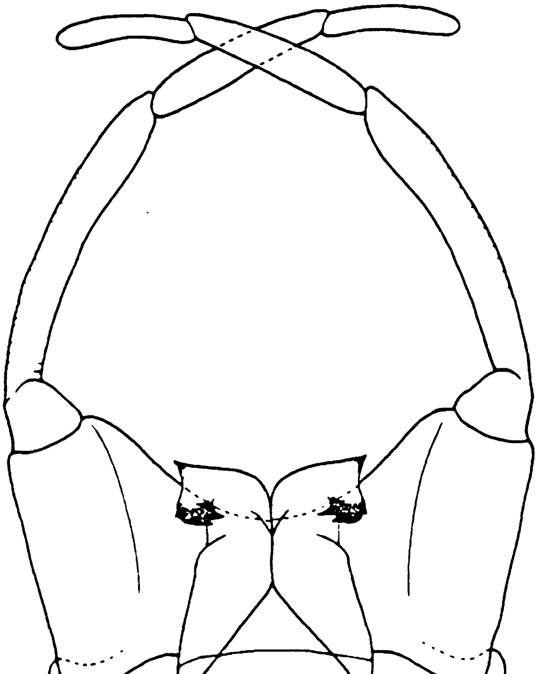

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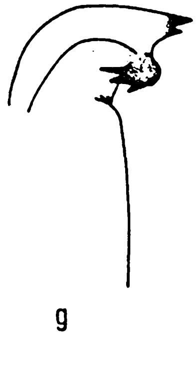

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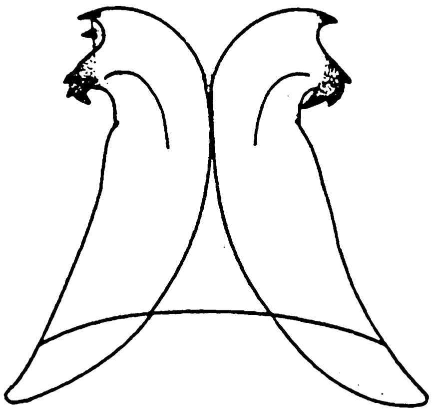

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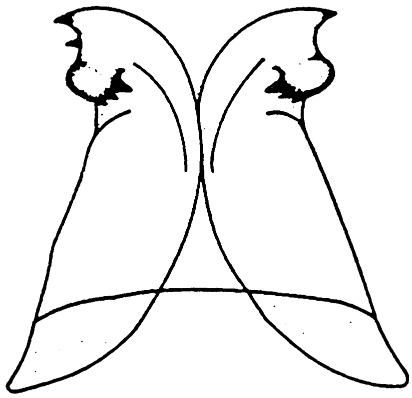

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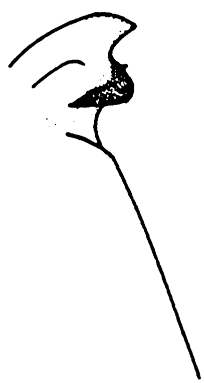

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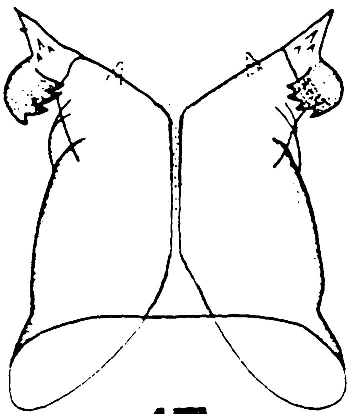

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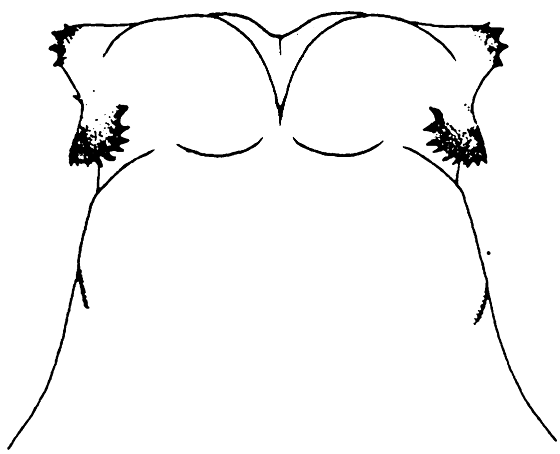

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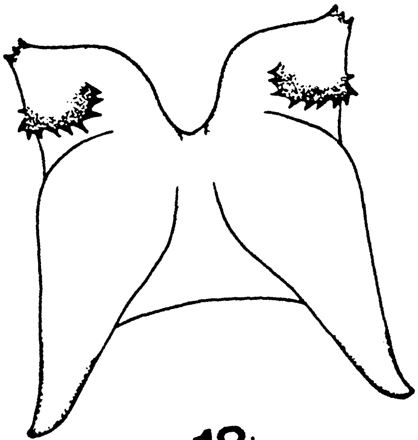

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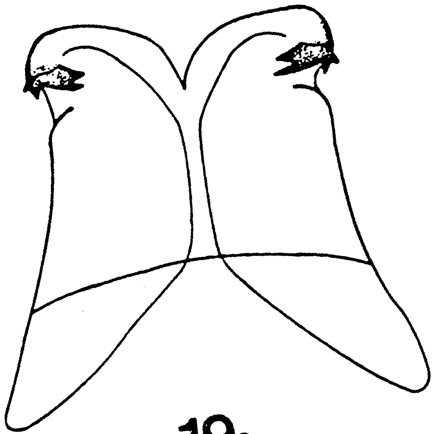

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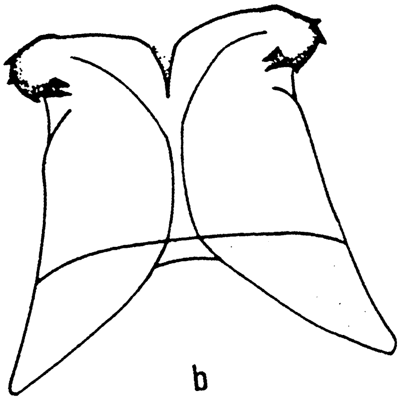

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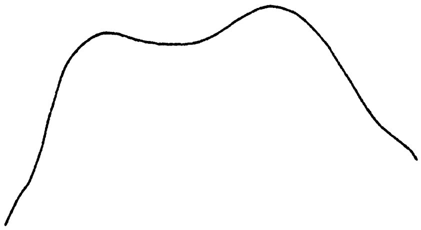

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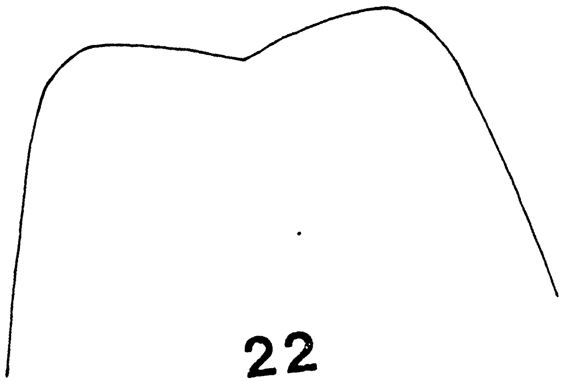

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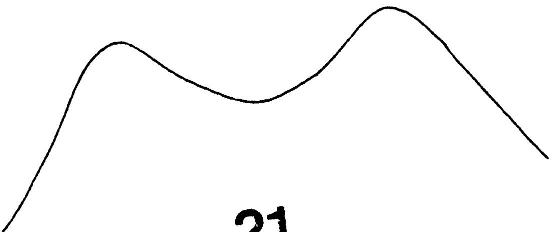

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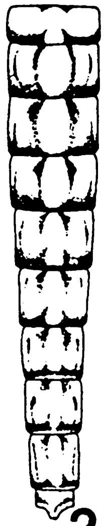

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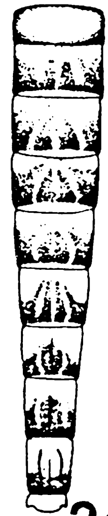

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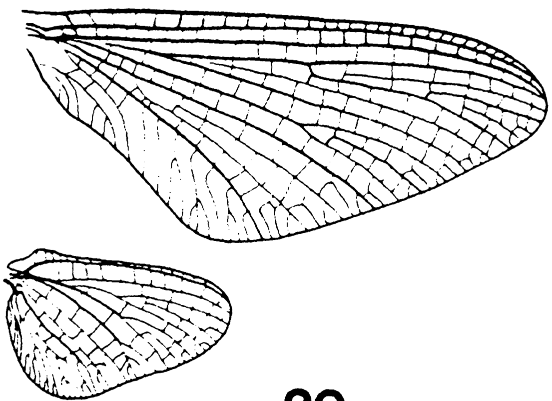

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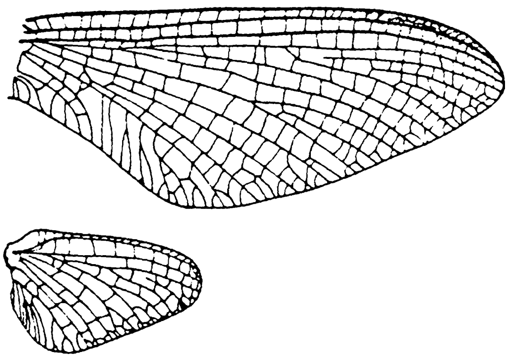

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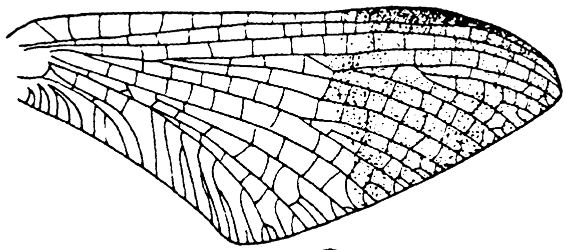

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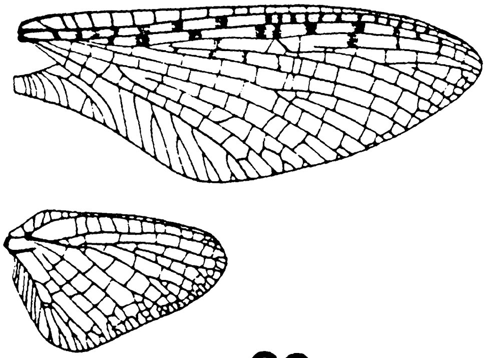

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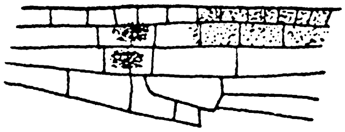

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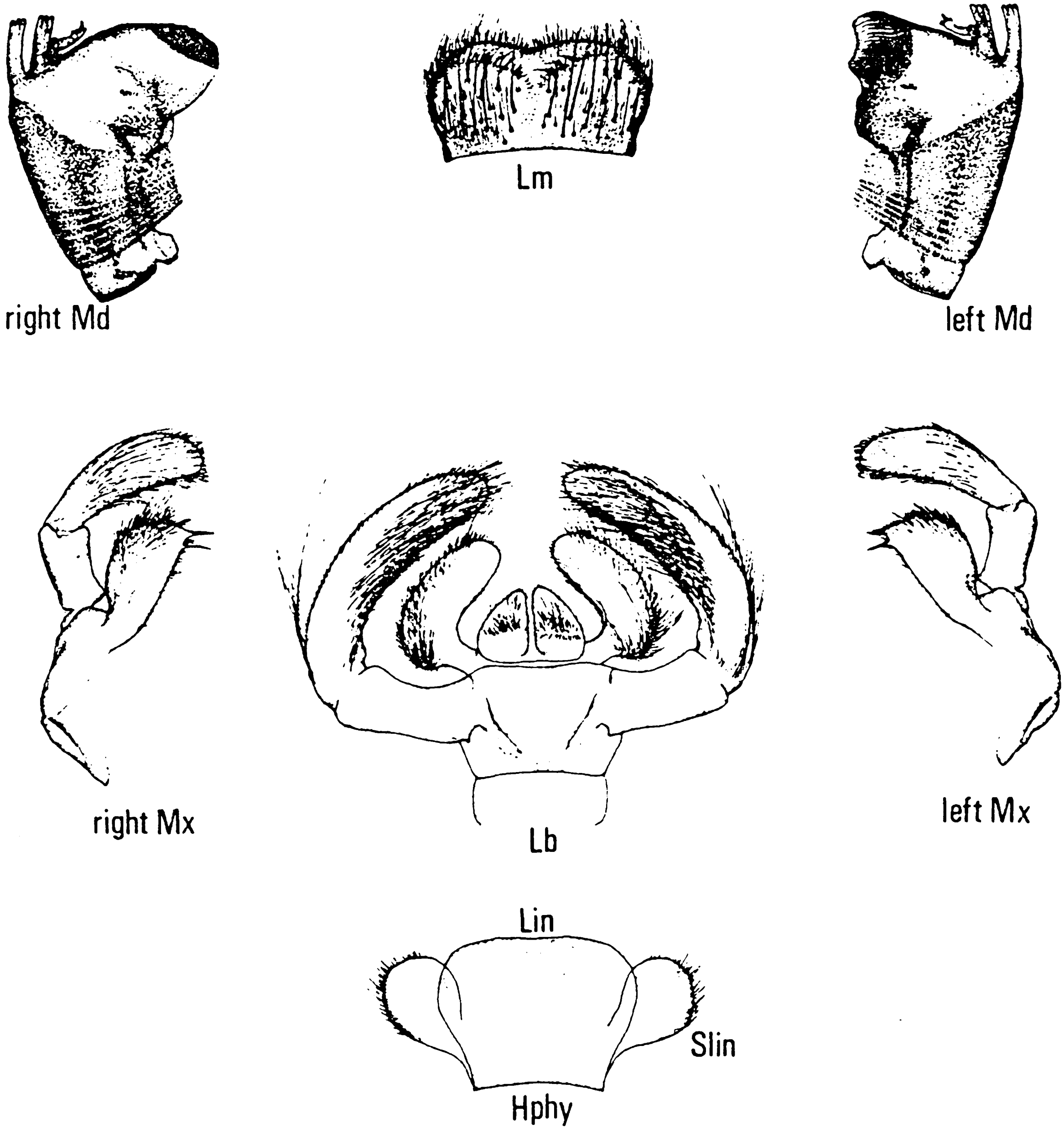

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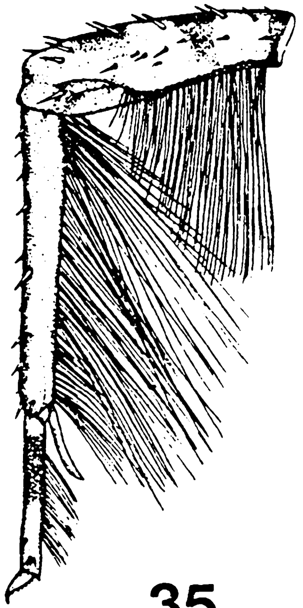

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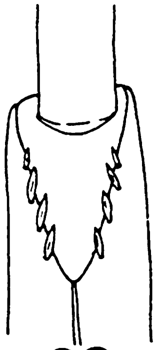

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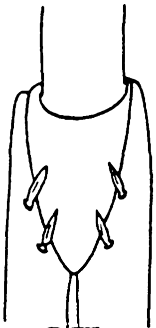

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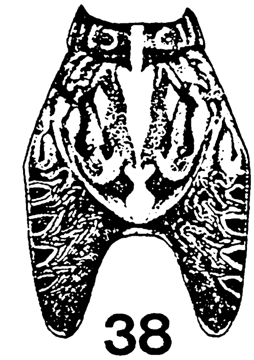

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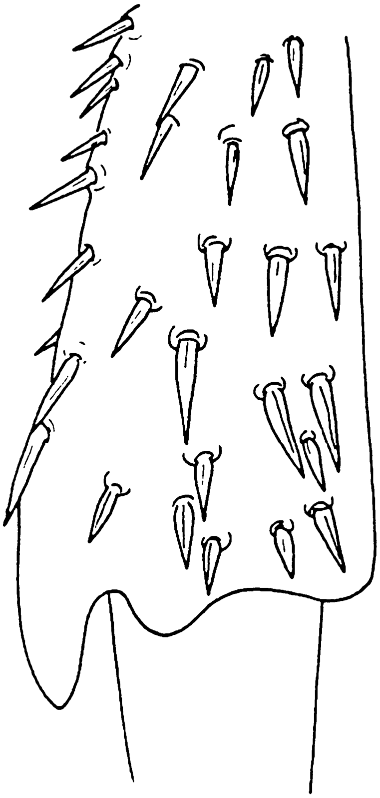

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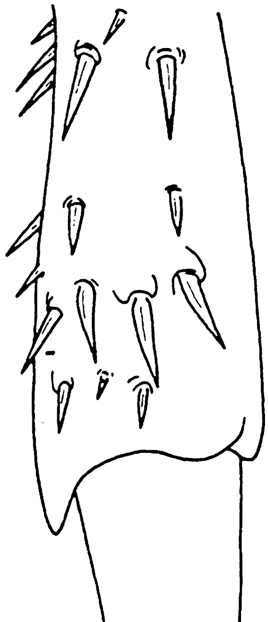

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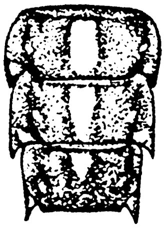
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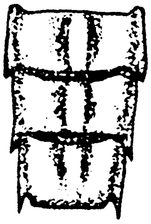
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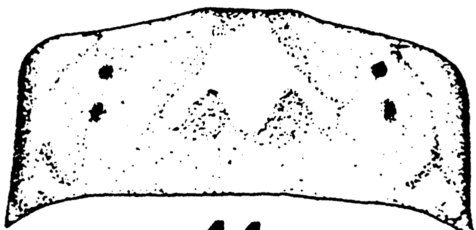
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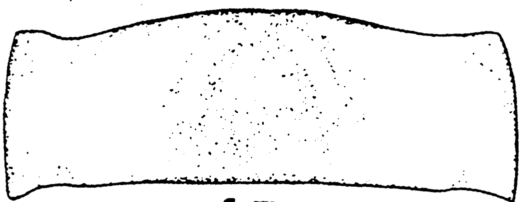
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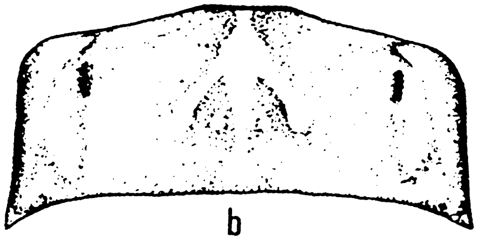
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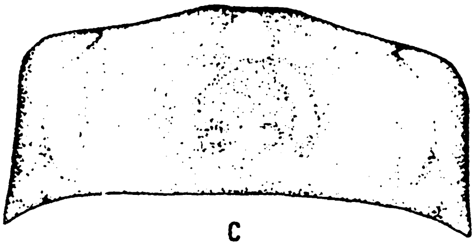
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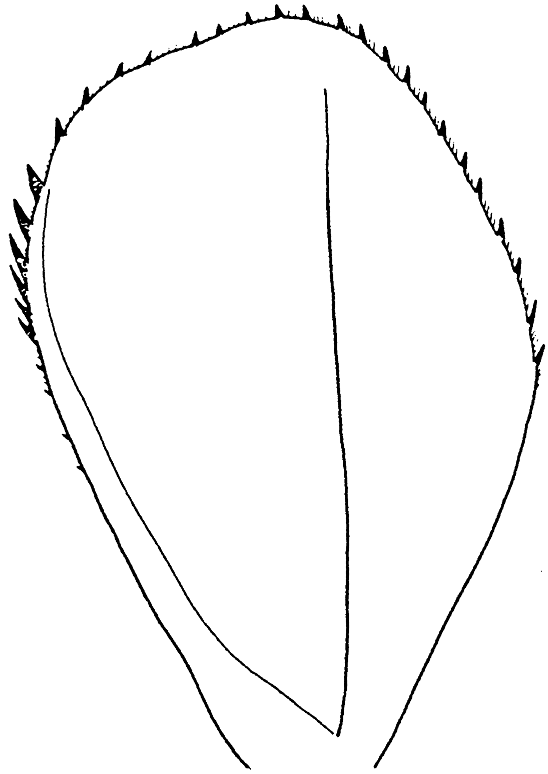
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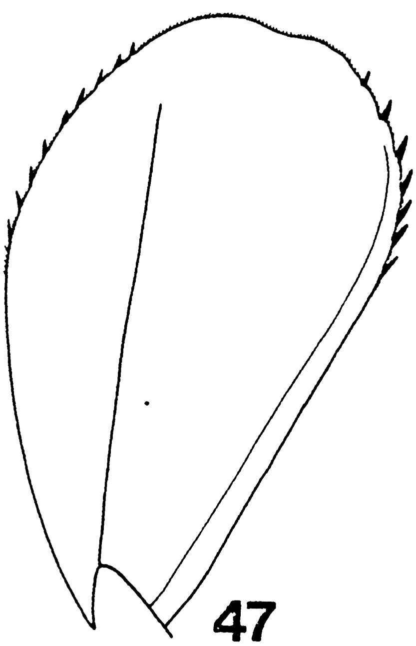
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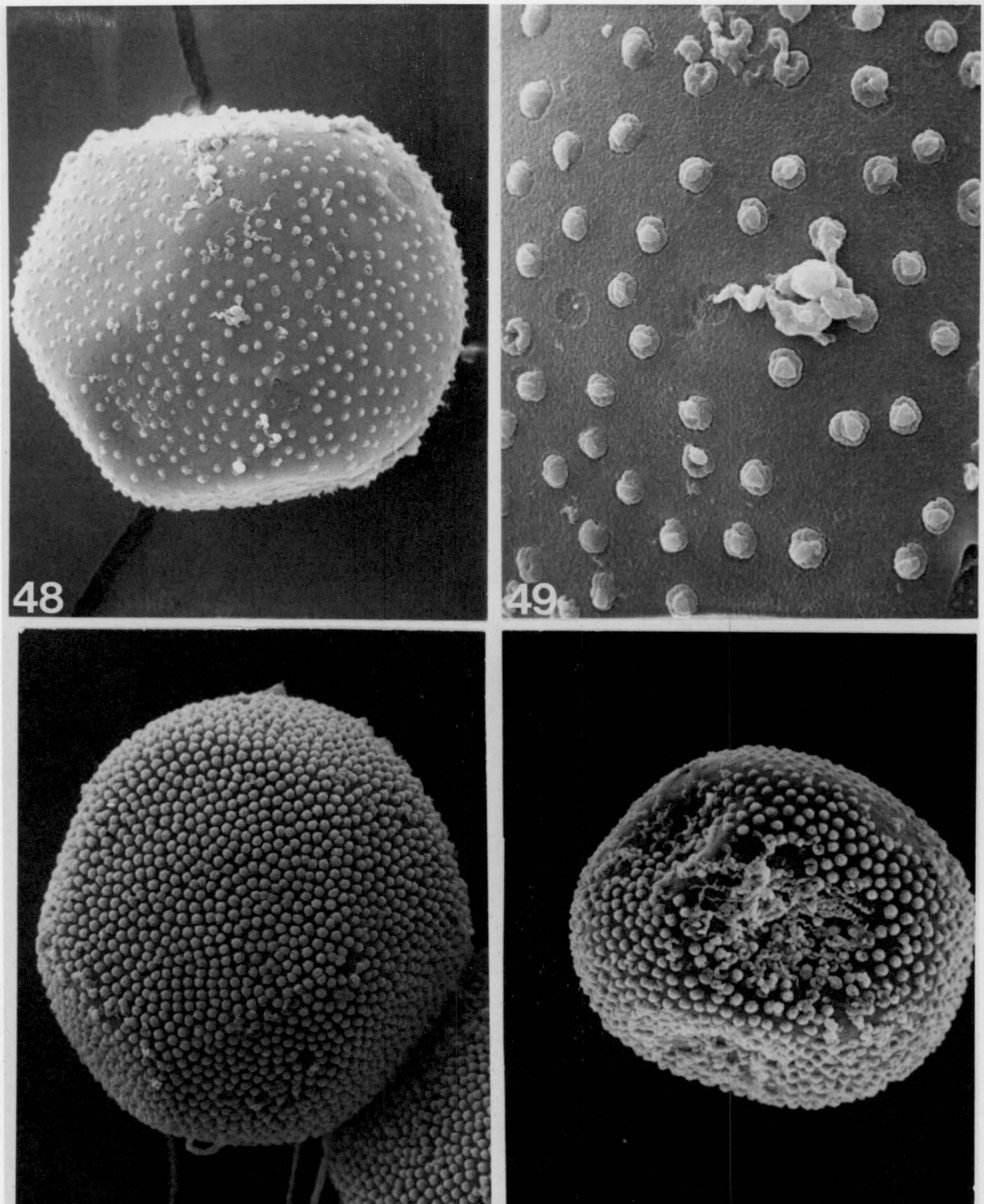
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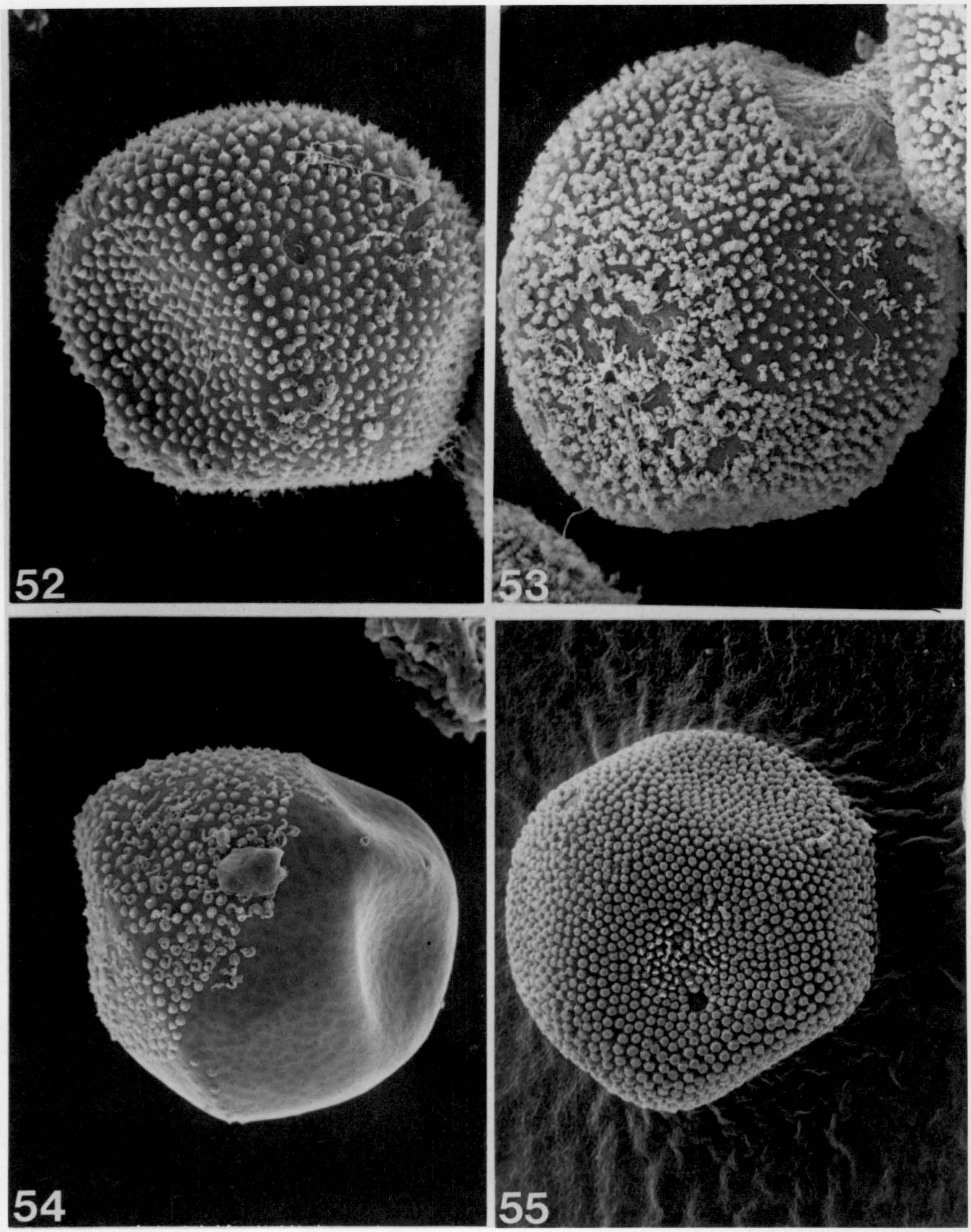
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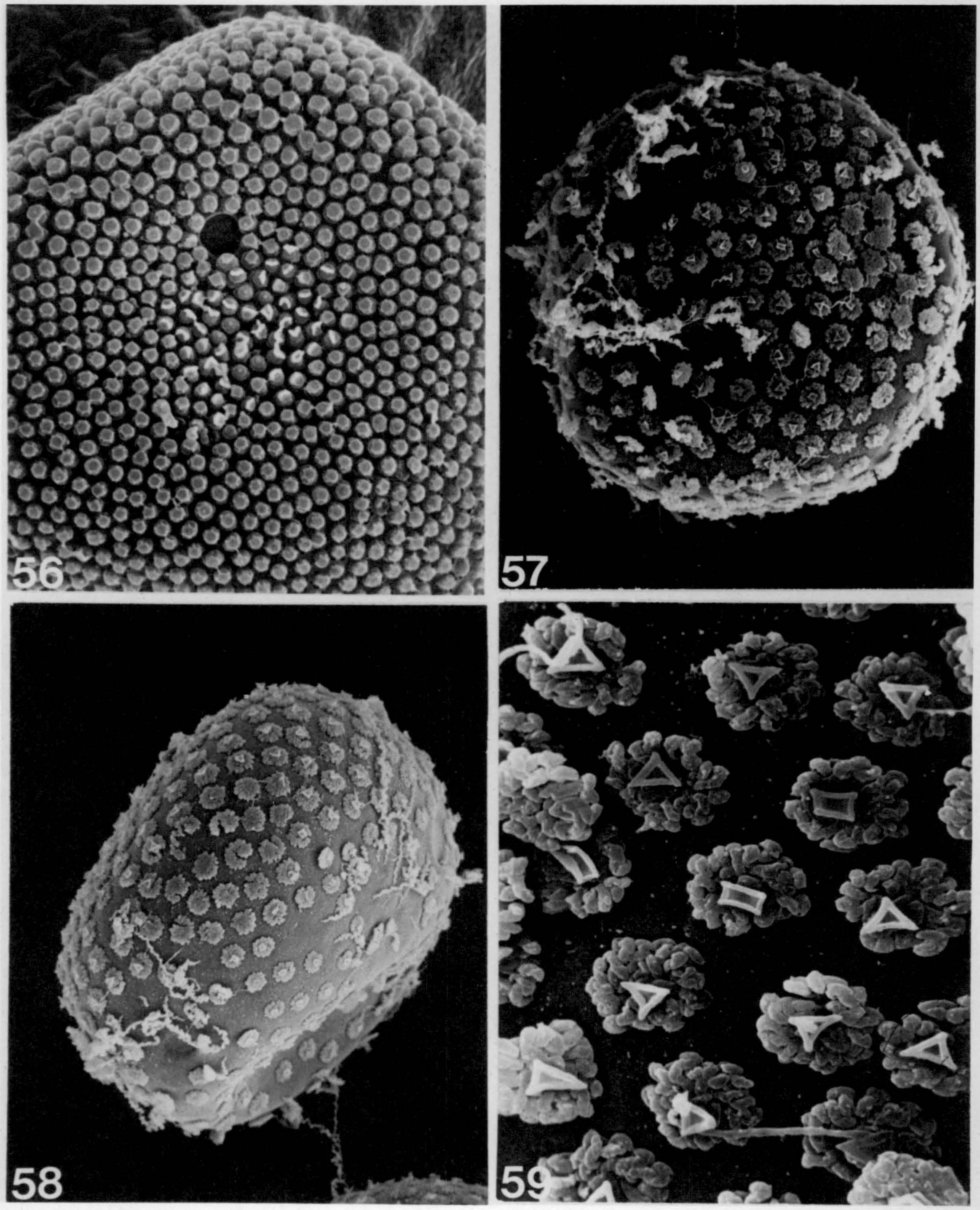
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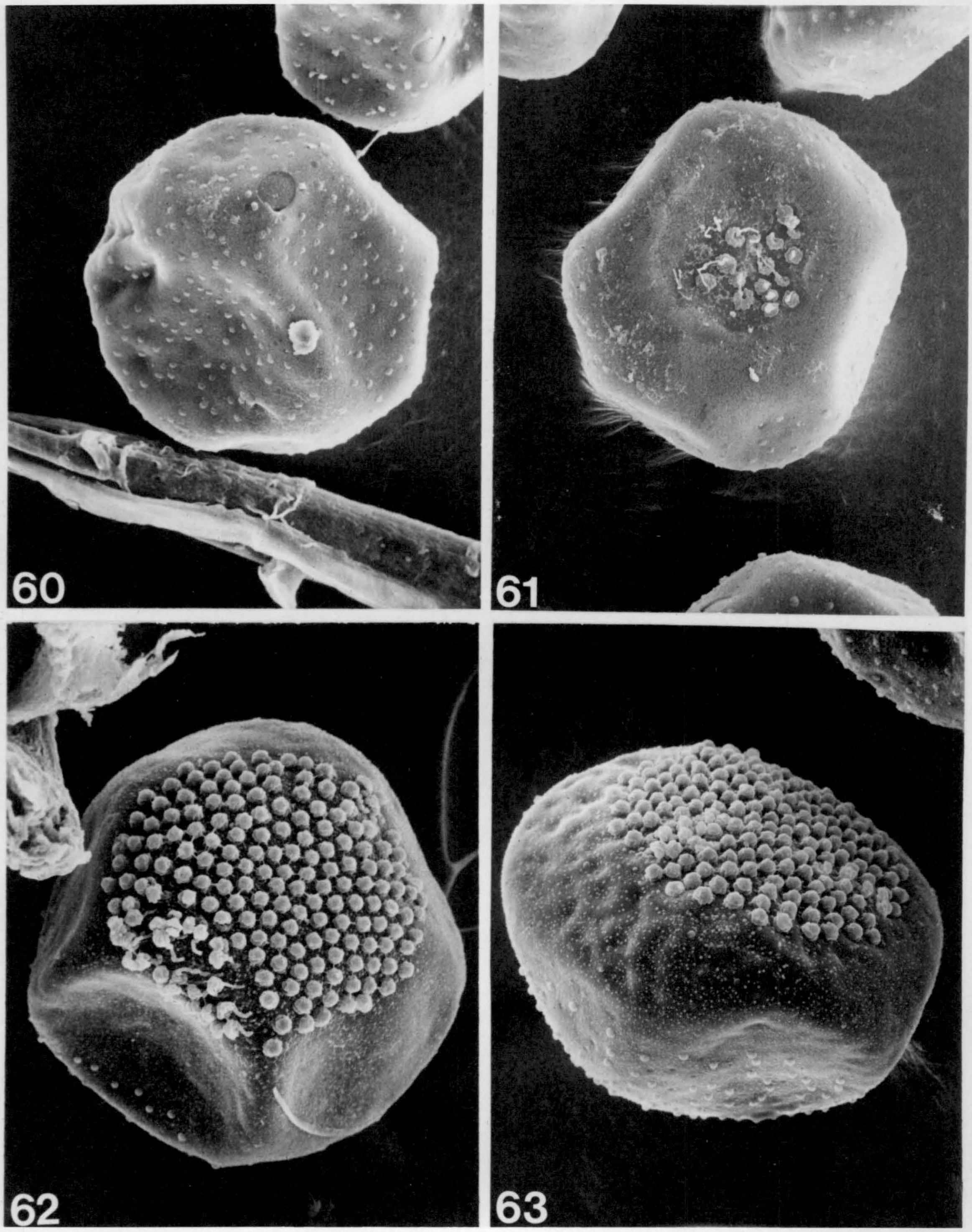
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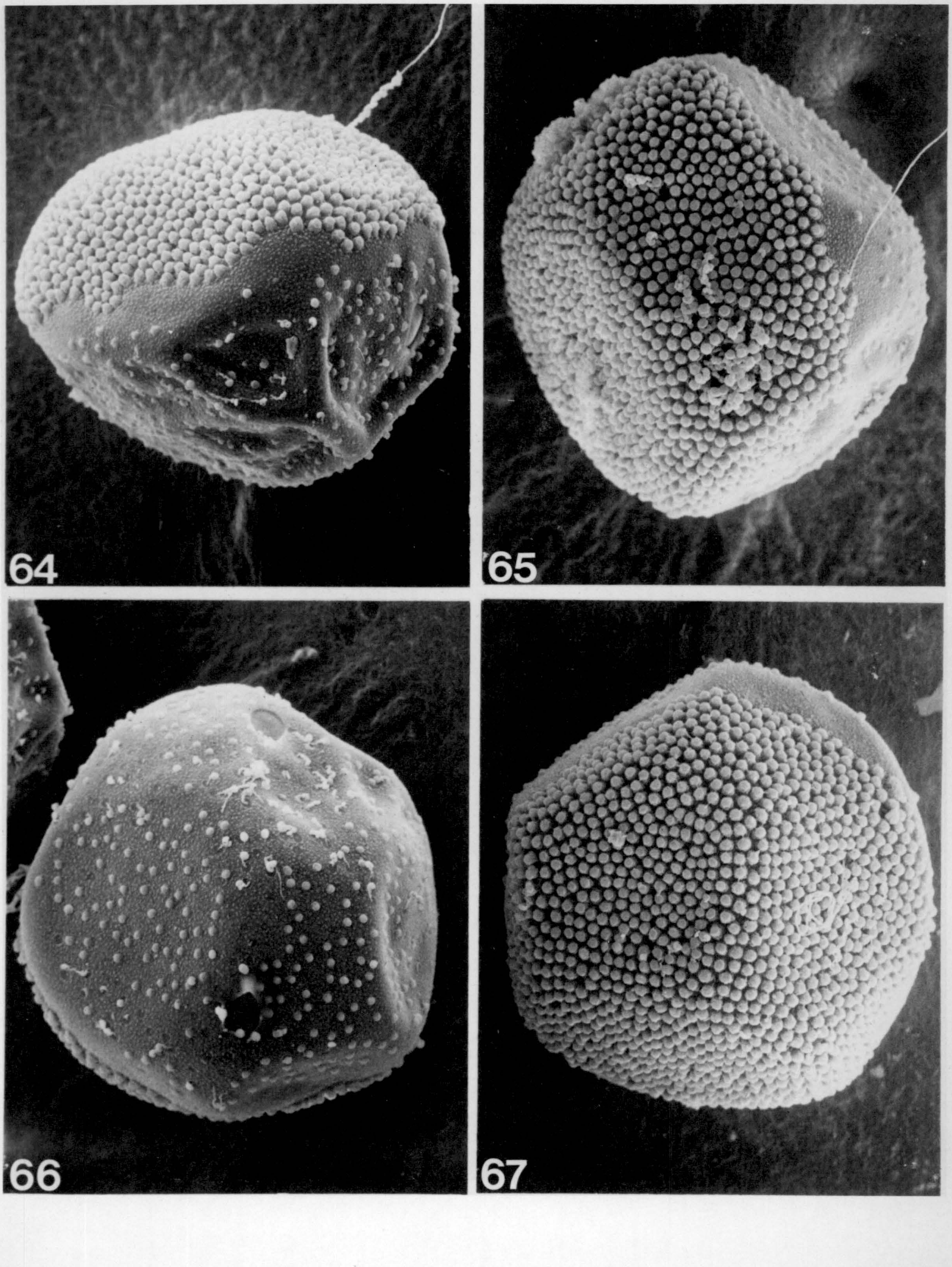
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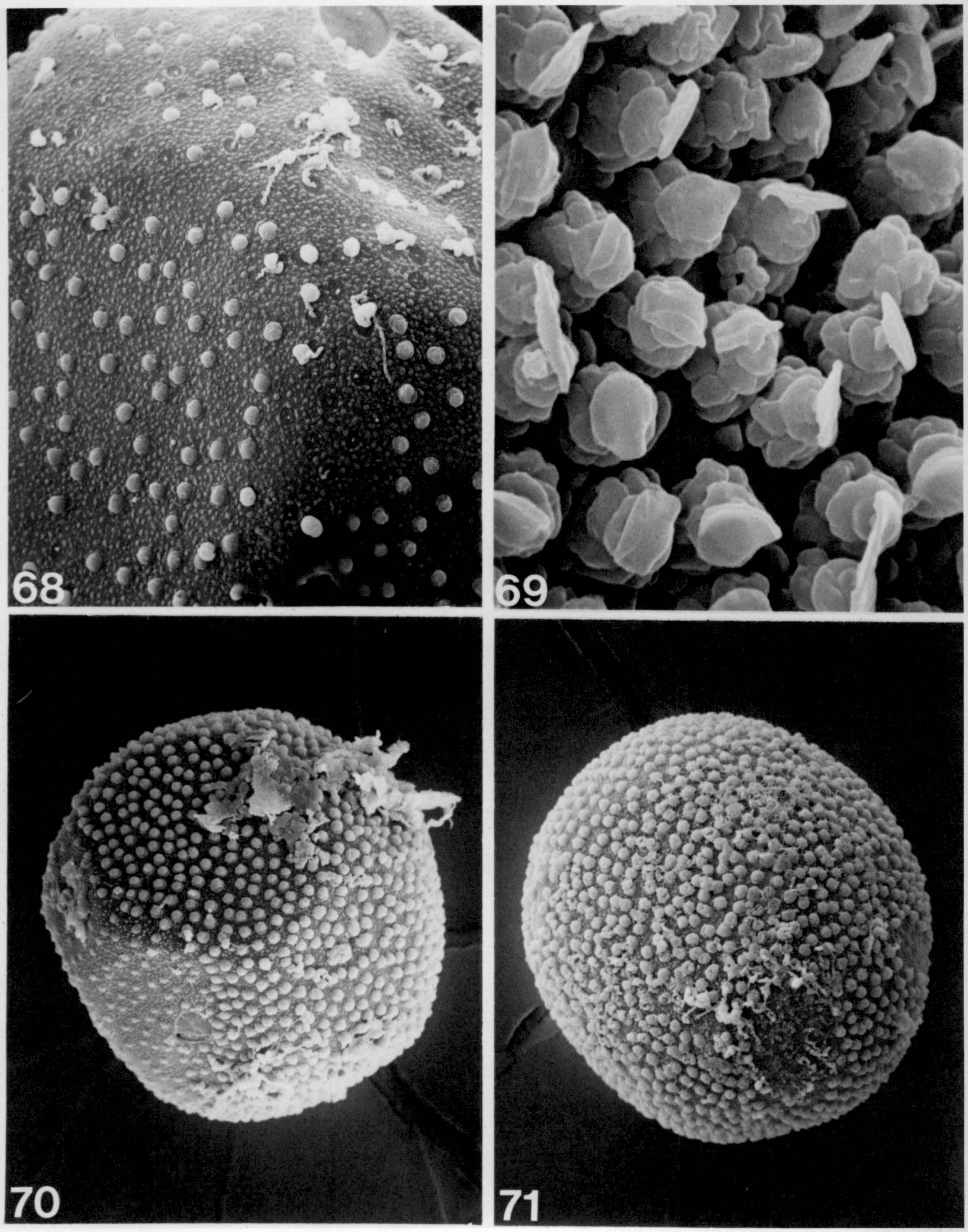
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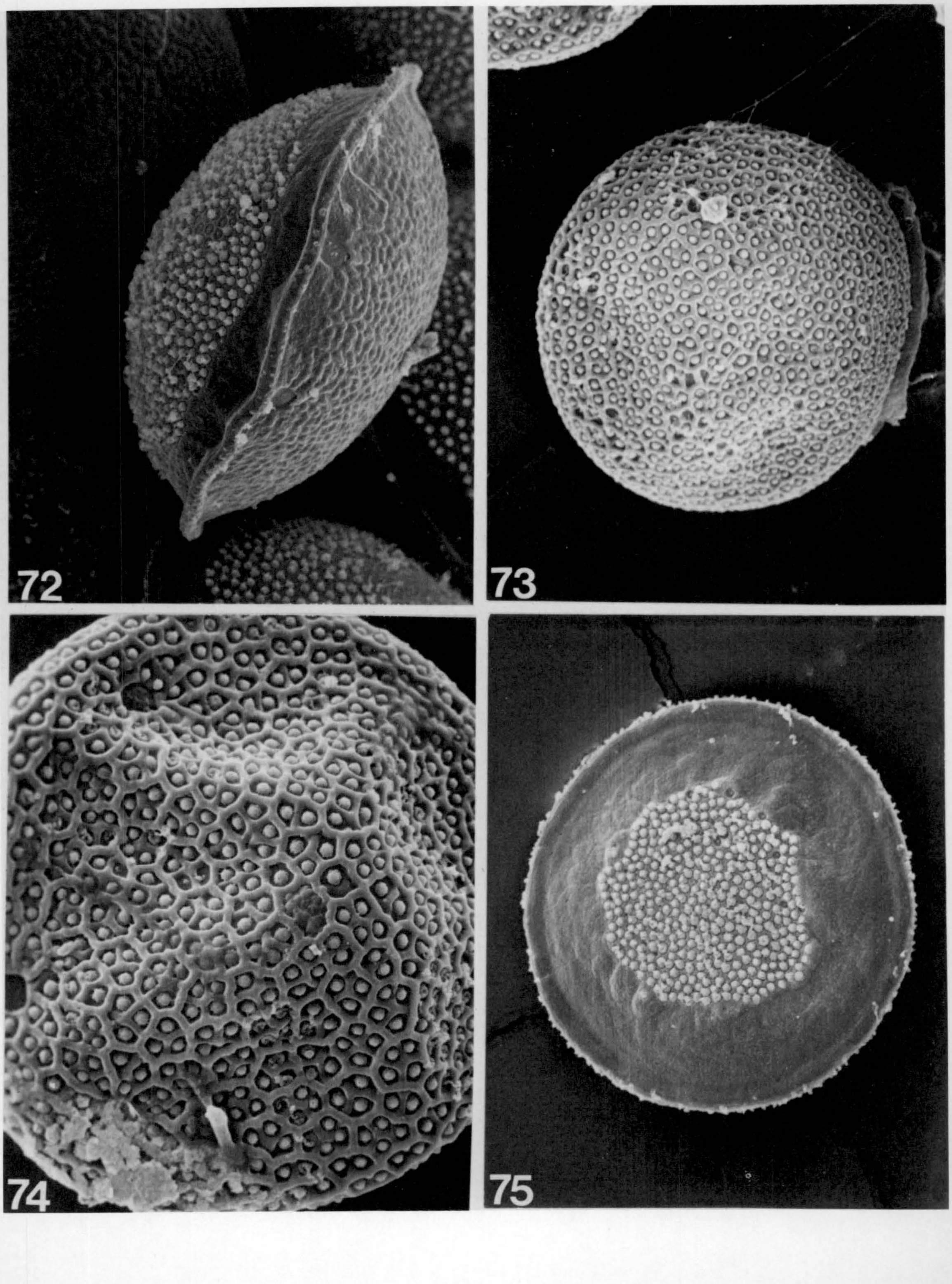
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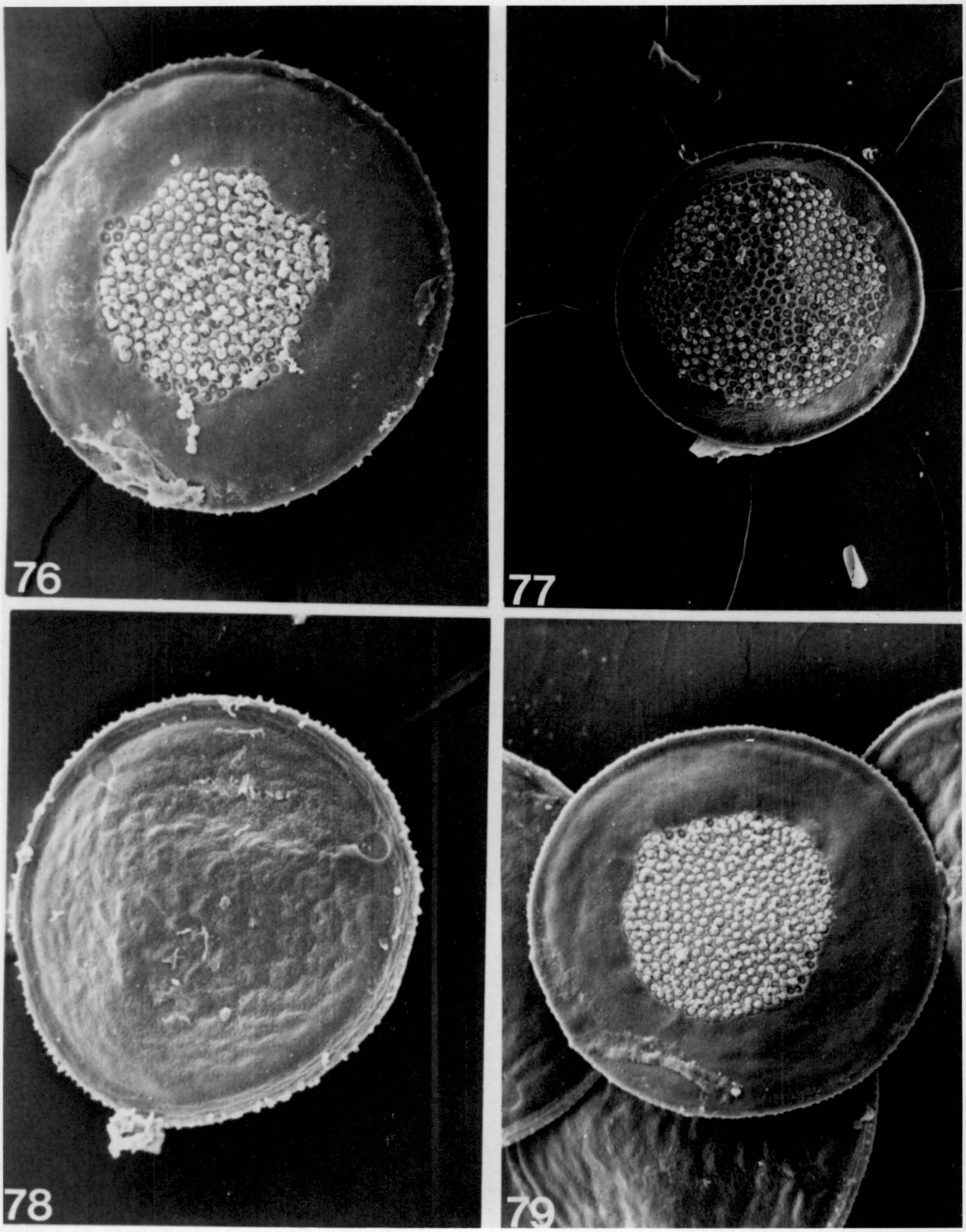
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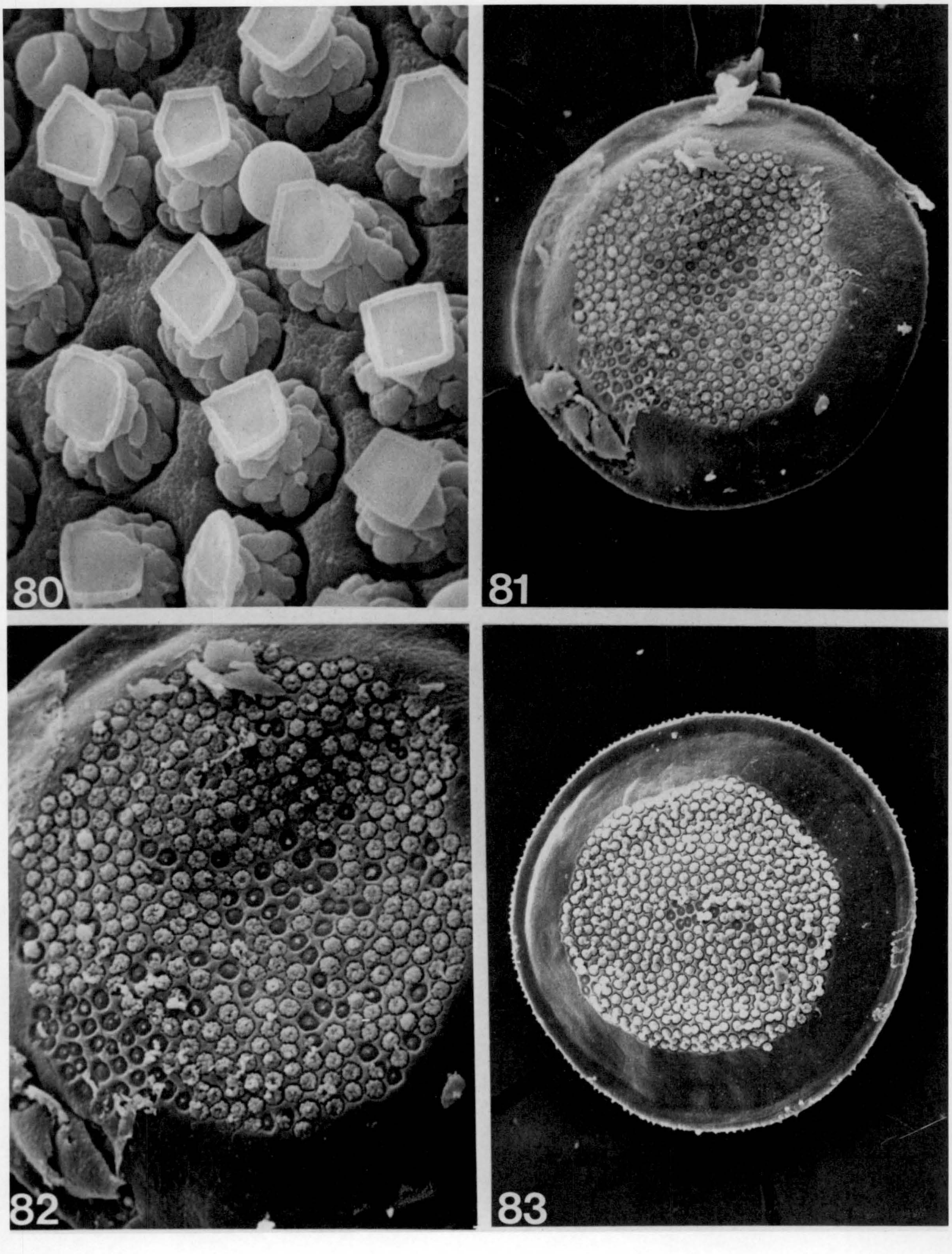
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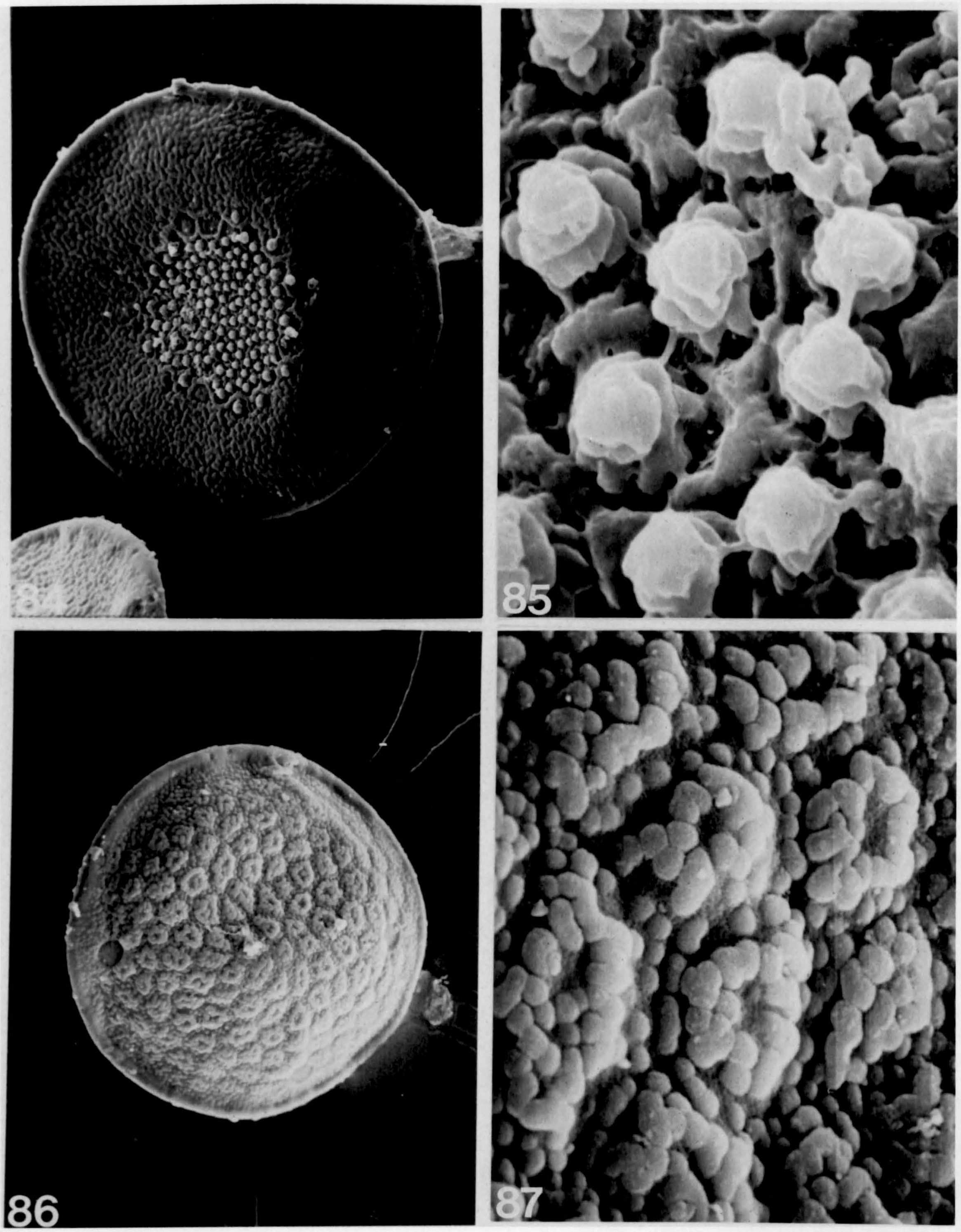
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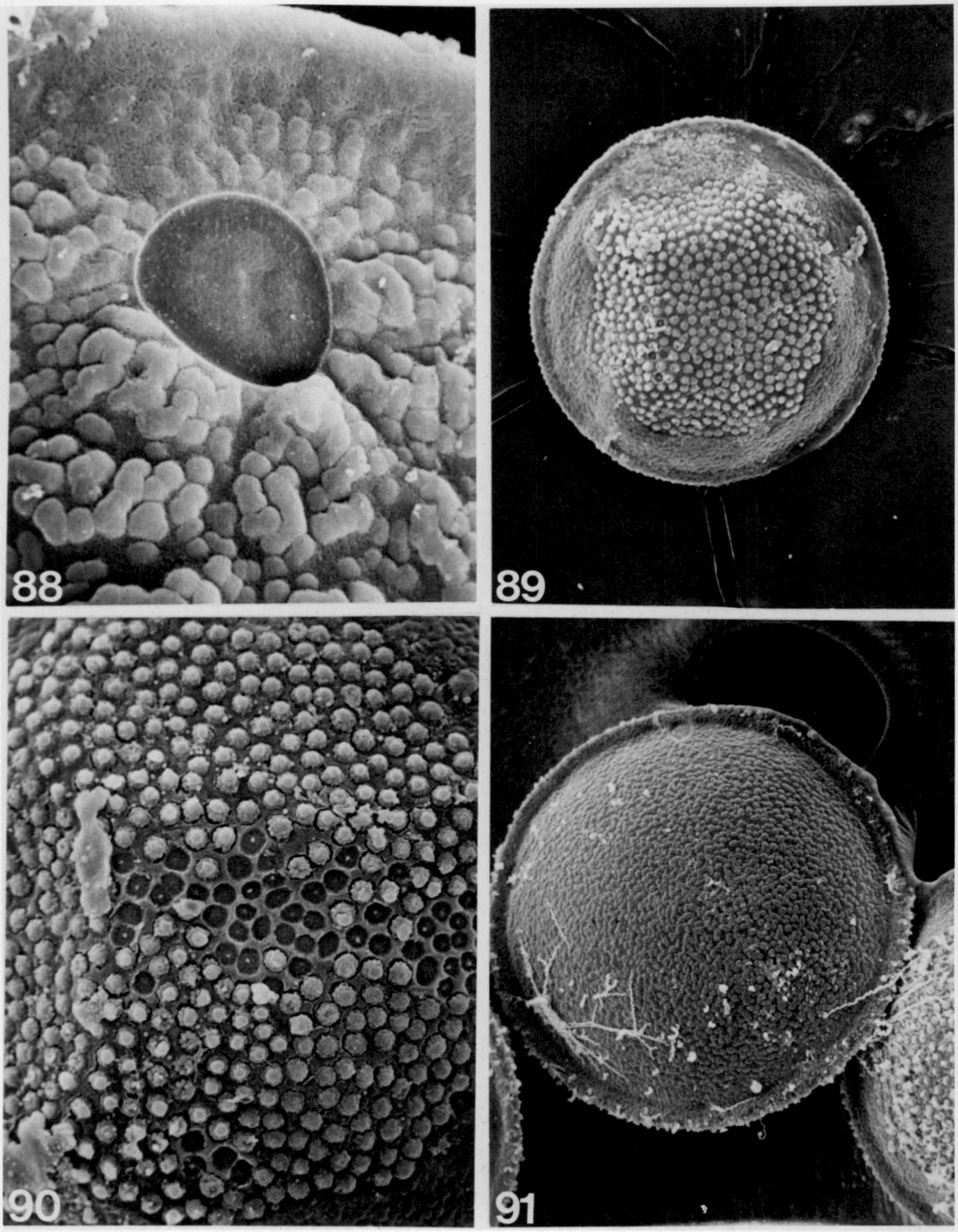
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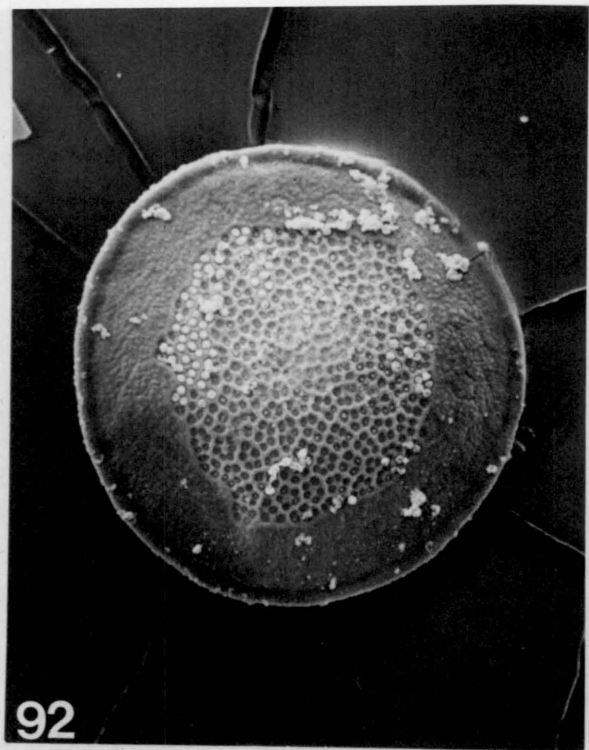
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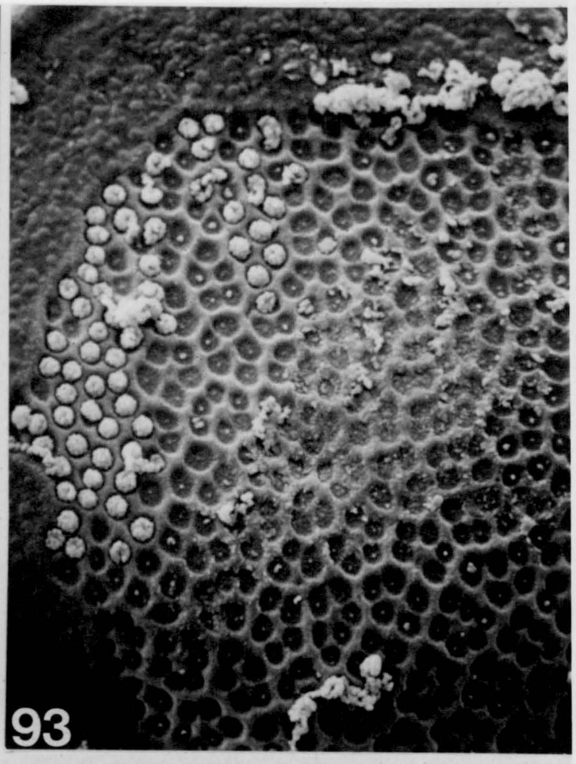
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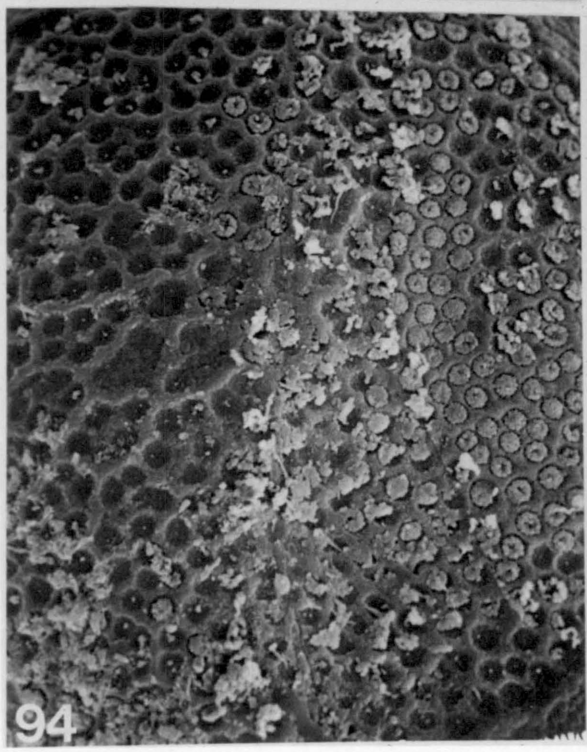
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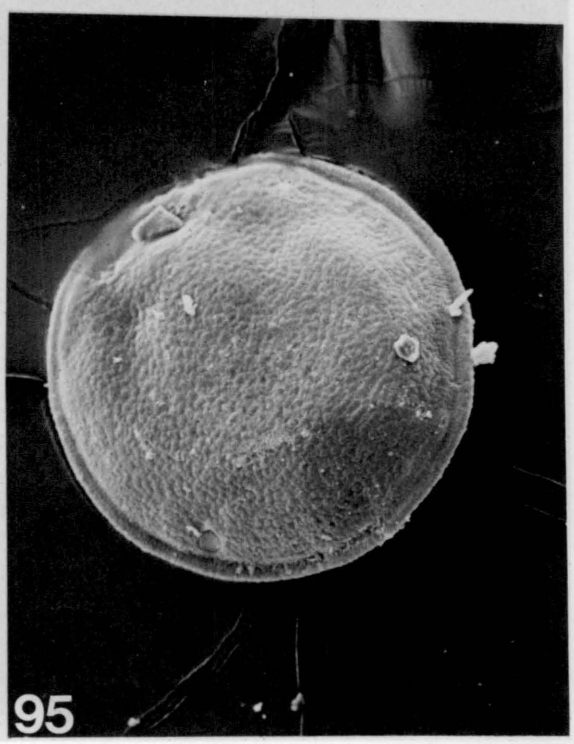
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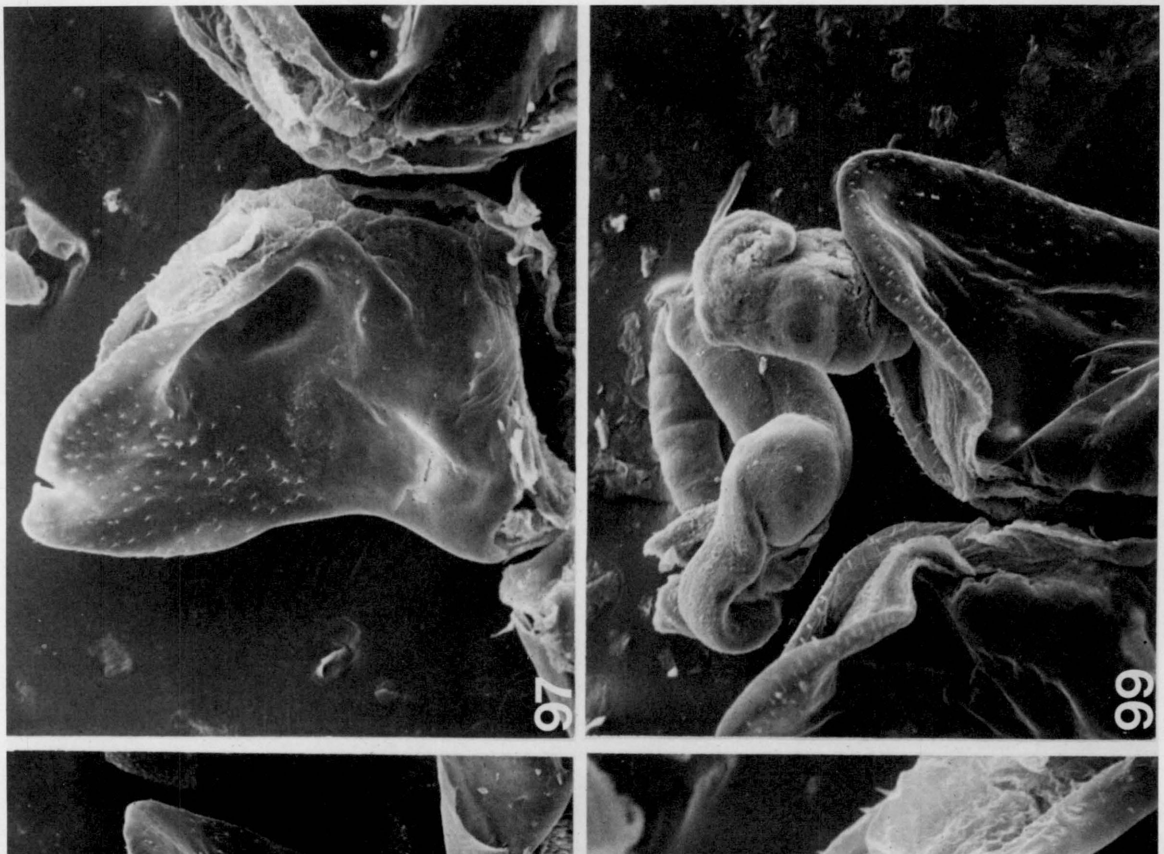
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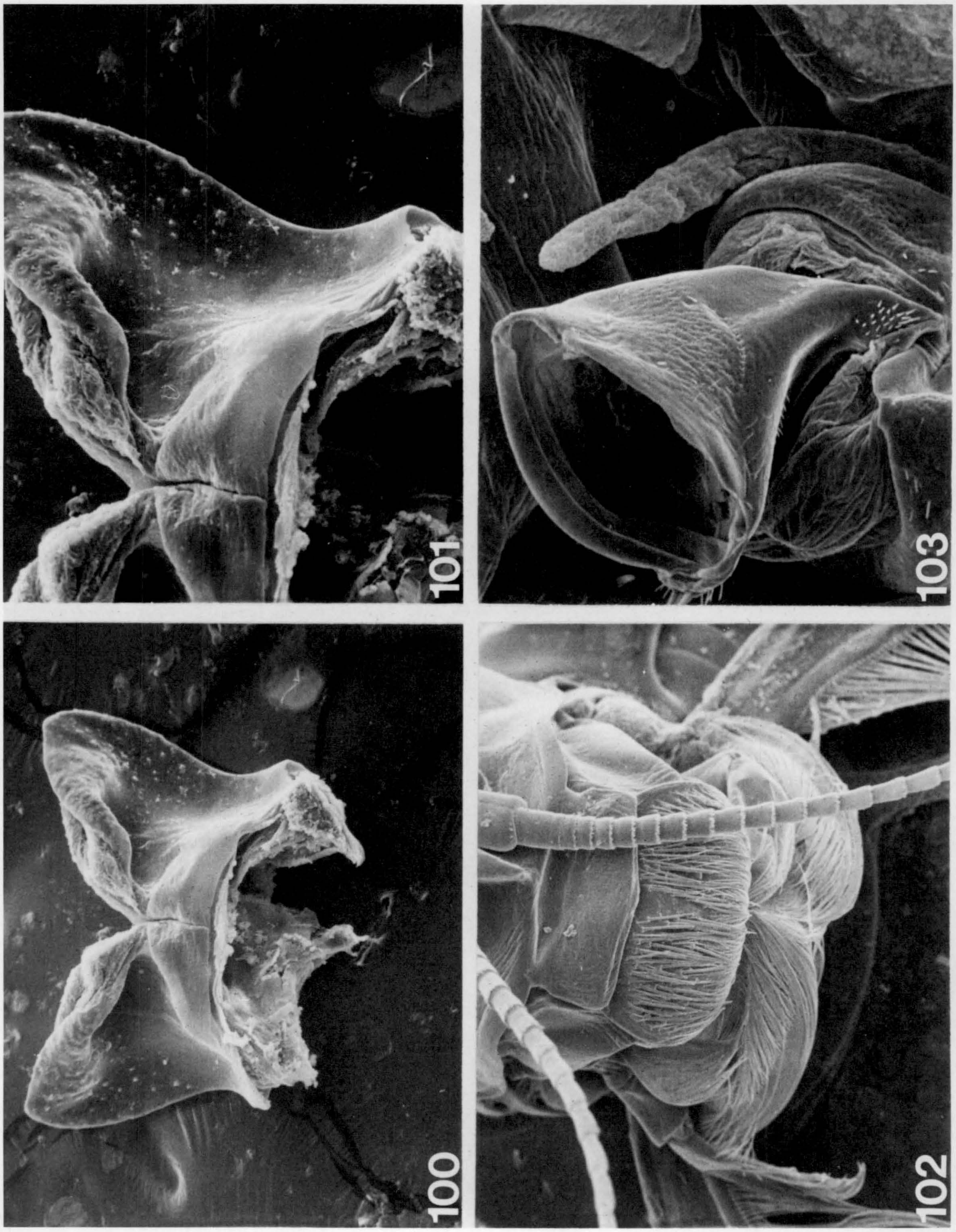
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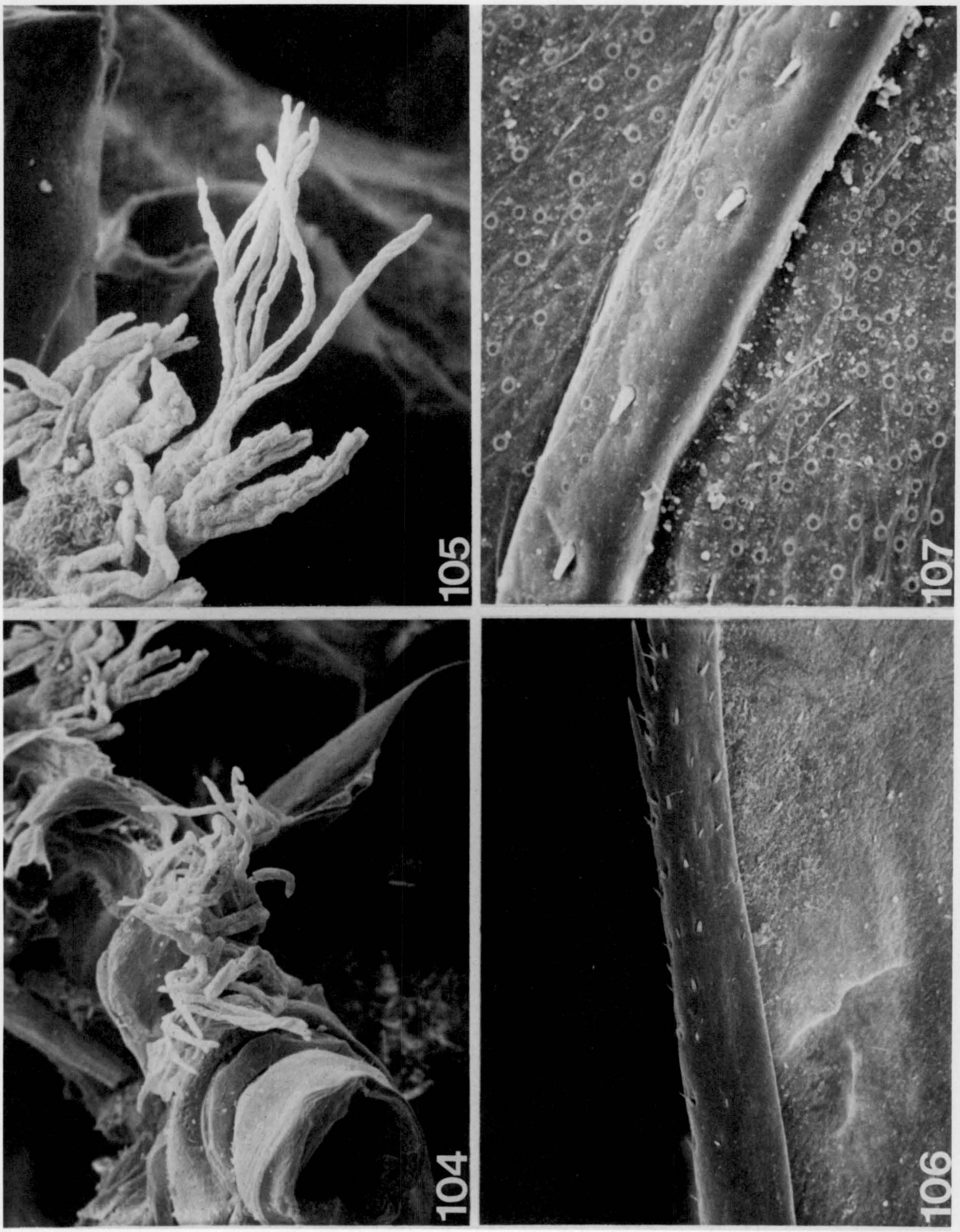
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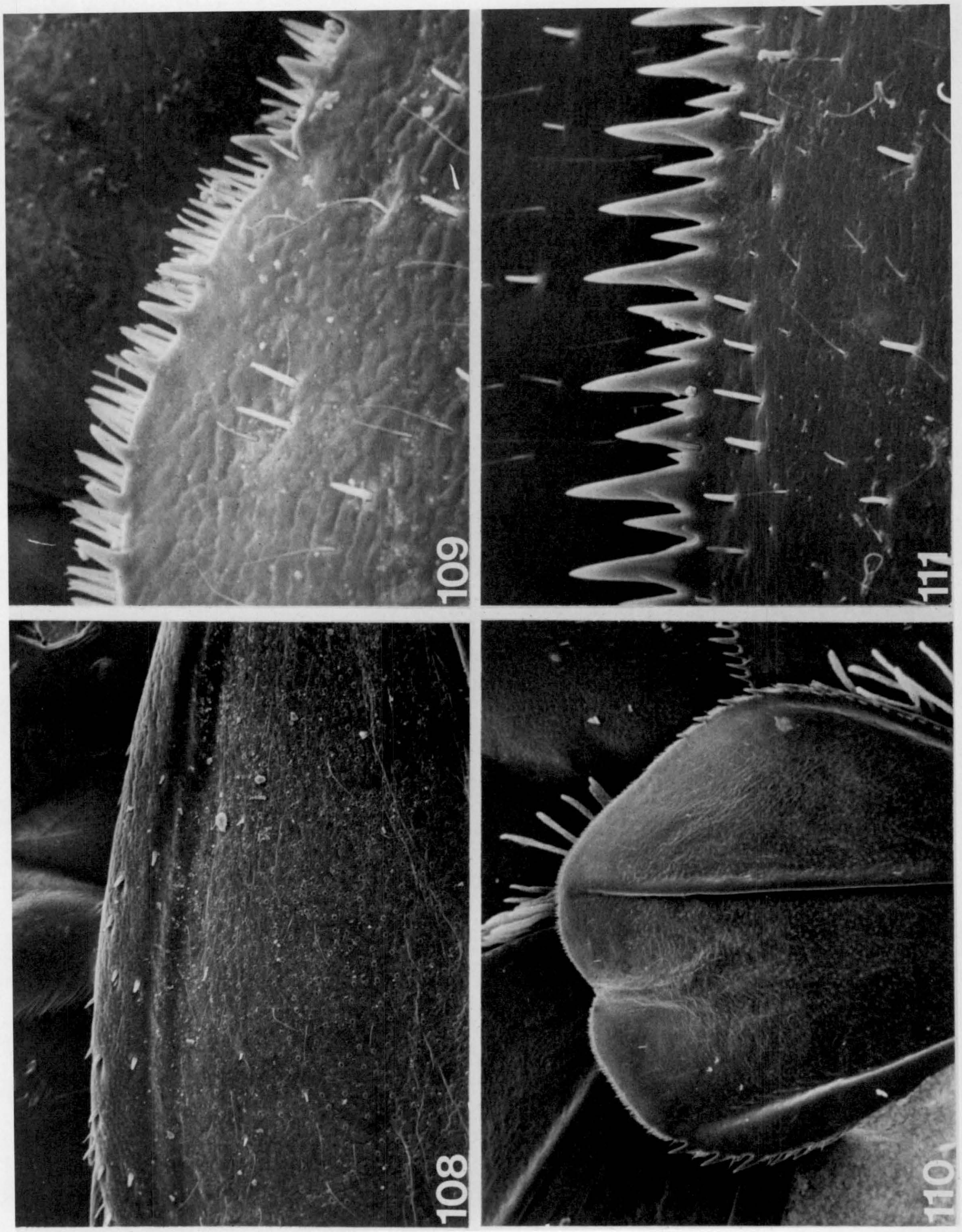
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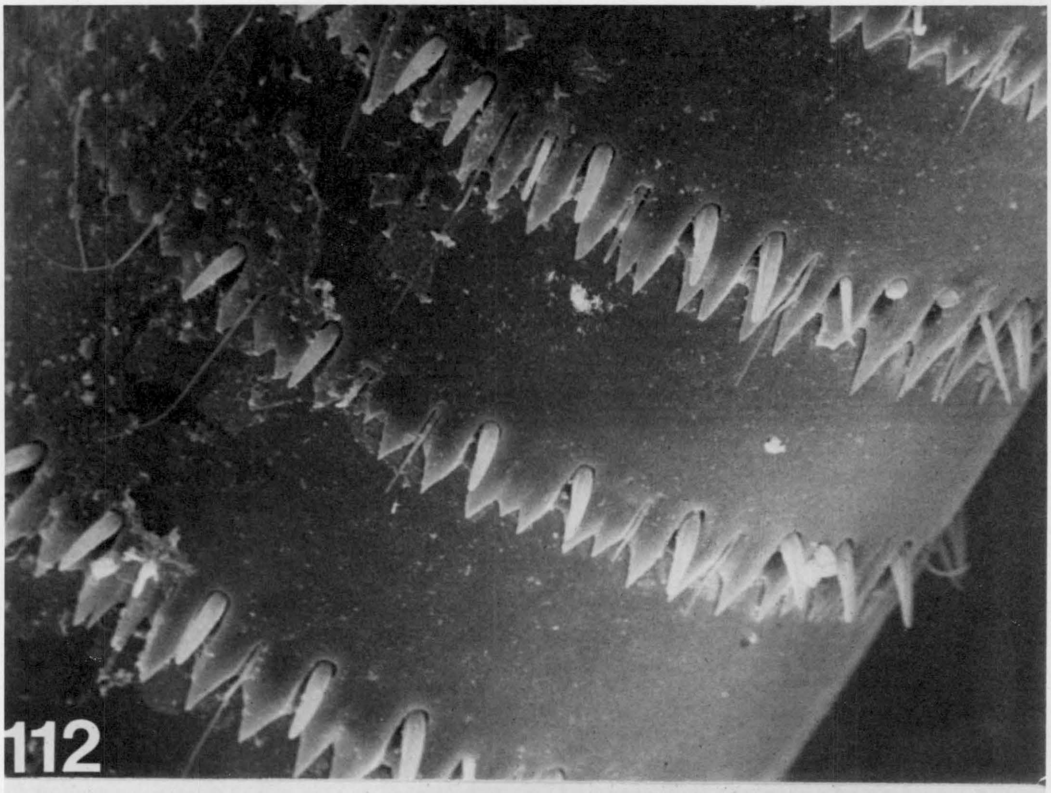

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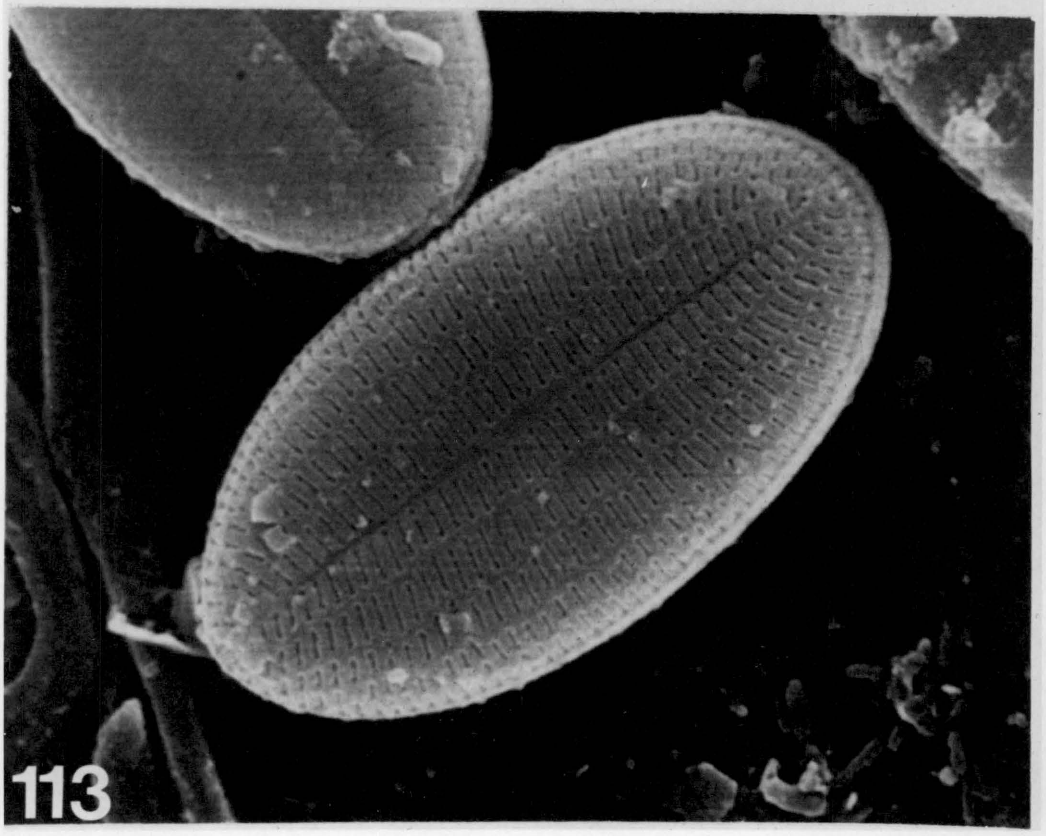

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PUBLICATIONS (refereed on original research):

1. Kondratieff, B. C. and J. W. S. Foster, III. 1977. Some Mayflies of Middle and East Tennessee. J. Tenn. Acad. Sci. 52:112.

2. Kondratieff, B. C. 1978. Ceratomia hageni: A new record (Lepidoptera: Sphingidae). News Lepid. Soc. 2:13.

3. Kondratieff, B. C. and J. R. Voshell. 1979. A new species of Diploperla (Plecoptera: Perlodidae) from Virginia. Ann. Entomol. Soc. Amer. 72:451-453.

4. Kondratieff, B. C. and J. R. Voshell. 1979. A checklist of the stoneflies (Plecoptera) of Virginia. Entomol. News 90:241-246.

5. Nelson, C. and B. C. Kondratieff. 1980. Description of a new species of Alloperla (Plecoptera: Chloroperlidae) from Virginia. J. Kansas Entomol. Soc. 53:801-804.

6. Kondratieff, B. C. and J. R. Voshell, Jr. 1980. Life history and ecology of Stenonema modestum in a southeastern piedmont stream (Ephemeroptera: Heptageniidae). Aquat. Insects 3:177-189.

7. Kondratieff, B. C. and J. R. Voshell, Jr. 1981. Influence of a reservoir with surface-release on the life history of the Mayfly Heterocloeon curiosum (McDunnough) (Ephemeroptera: Baetidae). Can. J. Zool. 59:305-314.

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A Biosystematic Revision

of the

Nearctic Species of the Mayfly genus *Isonychia*

(Ephemeroptera: Oligoneuriidae)

by

Boris Carl Kondratieff

(ABSTRACT)

The Nearctic species of the genus *Isonychia* Eaton are revised. Eighteen species are recognized, of which three are described as new; eleven species names are placed in synonymy. *Isonychia* *campestris* McDunough is recognized as a fully valid geographically restricted species. Two subgenera, *Isonychia* sensu stricto and *Prionoides* Kondratieff and Voshell are recognized on the basis of adult and nymphal characteristics. *Isonychia* s.s. includes four species groups: *bicolor* group with four species, *arida* group with one species, *sicca* group containing five species, and *diversa* group with one species. The subgenus *Prionoides* includes seven species. A Neotype is designated for *I*. *arida* (Say). Previously undescribed characters of the nymphal gills are described and illustrated. The male genitalia and eggs are illustrated for every species. The distribution of each species is mapped. Diagnostic keys to male adults and nymphs are presented. A discussion of the nomenclatural history of the genus and each species is included. Diagnostic characters, rearing and collecting techniques are also discussed.

The life histories and life cycles of two populations of *Isonychia* (*Isonychia*) *bicolor* (Walker) and one population of *Isonychia* (*Prionoides*) *obscura* Traver are presented in detail. Many features used in the past as specific criteria, especially in the *bicolor* and *sicca* Groups are found to be related to developmental periods of given populations involving geography, elevation, water temperature and stream size. The life cycle of *I*. *bicolor* is probably bivoltine at both sites. At the trout stream site there is a large-sized spring emerging generation and a much smaller summer emerging generation with considerable overlap. *Isonychia* *obscura* Traver is univoltine with adult emergence in mid-June and with egg diapause during the summer months. Additional life history information is also presented for *I*. (*I*.) *tusculanensis* Berner and *I*. (*P*.) *serrata* Traver.

The evolution of the genus _Isonychia_ and the two subgenera _I_. (_Isonychia_) and _I_. (_Prionoides_) is hypothesized. The North American biogeography of _Isonychia_ may have included an invasion of North America via the "asiamerican" land mass of the Cretaceous. The early _Isonychia_ mayflies may have been adapted to low order cool streams of high elevations. This lineage was probably similar to the subgenus _Prionoides_. _Isonychia_ s.s. has been successful in colonizing the upper and lower austral zones and appears to be a warm water adapted group.