

SUBGENERIC AND SPECIES-GROUP CLASSIFICATION OF THE
MAYFLY GENUS *ISONYCHIA* IN NORTH AMERICA
(EPHEMEROPTERA: OLIGONEURIIDAE)

BORIS C. KONDRATIEFF AND J. REESE VOSHELL, JR.

Department of Entomology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061.

Abstract.—The mayfly genus *Isonychia* Eaton is divided into two subgenera, *Isonychia* s.s. and *Prionoides*, new subgenus, based on distinct morphological features of adults and nymphs of the Nearctic species. *Isonychia* s.s. is divided into four species groups based on penes form of male imagoes. Descriptions and keys to these subgenera and species groups are provided. *Isonychia pictipes* Traver is a new synonym of *Isonychia arida* (Say). Preliminary assignment is also given for the Palearctic, Oriental, and Neotropical species.

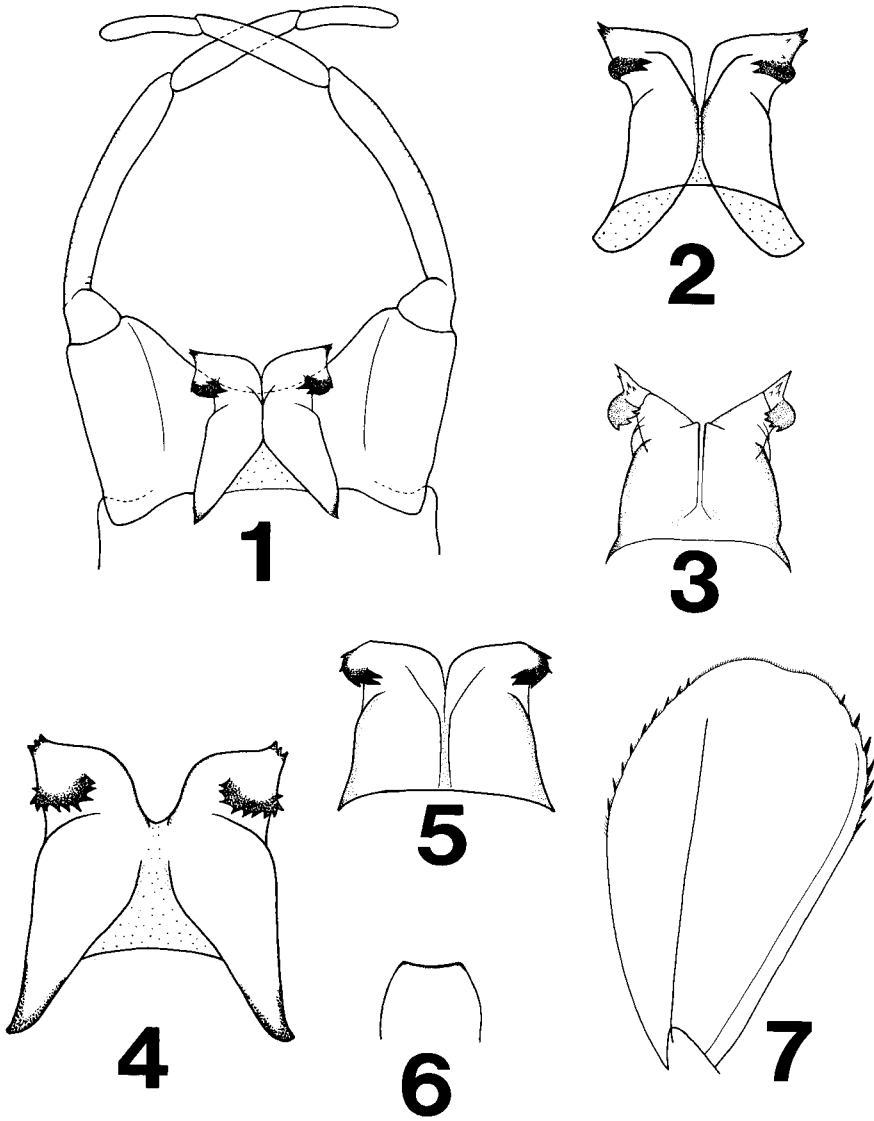
The genus *Isonychia* includes approximately 38 species, of which 27 are Nearctic (Edmunds et al., 1976). The remaining species are Palearctic, Oriental, or Neotropical.

McDunnough (1931) first suggested that the male imagoes of the North American species of *Isonychia* could be readily divided into two distinct groups. Traver (1932) termed these groups the “*arida*” (= *sayi* of Burks, 1953) and the “*albomanicata*” (= *bicolor* of McDunnough, 1931) groups. She further suggested that the “*albomanicata*” group may be subdivided into the *sicca* group using penes form. Traver (1935) and Burks (1953) noted that there were four distinct types of male penes in the Nearctic species.

A revision of the Nearctic species by the authors indicated, after careful study of imaginal, nymphal, and egg characters, that *Isonychia* consists of two monophyletic lineages. Using the criteria of Edmunds (1962), we herein recognize the two lineages as subgenera.

Terminology of egg structure follows Koss and Edmunds (1974). Eggs were removed from associated imago females because eggs of late instar nymphs and subimagoes usually were covered with suprachoronic adhesive layers (Koss and Edmunds, 1974; Kopelke and Müller-Liebenau, 1981). The ratio of the length of the second foretarsal segment to the first foretarsal segment is expressed as the foretarsal ratio. Other morphological terms follow Edmunds et al. (1976). Imagoes and nymphs of all Nearctic species were examined except *I. intermedia* Eaton, in which case only subimagoes and late-instar nymphs were available.

The Palearctic and Oriental species are poorly known. Most available figures of the male genitalia are ventral views, not illustrating important dorsal features. Therefore, the placement of all Palearctic and Oriental species in *Isonychia* s.s. are tentative. *Isonychia alderensis* Lewis is a fossil species from Montana (USA) known from Oligocene sediments.



Figs. 1-7. *Isonychia* (*Prionoides*). 1-5, Male genitalia, dorsal. 1, *I. annulata*. 2, *I. georgiae*. 3, *I. sayi*. 4, *I. serrata*. 5, *I. aurea*. 6, Subanal plate. 7, 7th nymphal gill.

Subgenus *Prionoides* Kondratieff and Voshell, NEW SUBGENUS

Type species.—*Isonychia georgiae* McDunnough.

Male imago.—Body length 9–17 mm, forewing 9–16 mm. General body color yellowish brown; median and submedian maculae on abdominal terga brownish or purplish, usually bordering a middorsal stripe; or abdominal terga dark brown with pale yellow anterolateral spots (*I. sayi*). Wings hyaline with veins and crossveins reddish brown to purplish black or with veins and crossveins whitish (*I. sayi*). Prothoracic leg with tarsal ratio .60–.88; femur, tibia, and tarsus brown to purplish brown. Meso- and metathoracic legs yellowish, tarsi sometimes tinged

with purple. Caudal filaments dark brown or pale with reddish brown articulations or whitish without dark articulations (*I. sayi*).

Male genitalia.—Subgenital plate broadly concave or with only slight posteromedian emargination (Fig. 1). Forceps sometimes appearing 5-segmented; length of segment 1 ranges from subequal to $\frac{1}{2}$ that of segment 2. Penes, dorsally with incurved medial flap with prominent sclerotized lateral and marginal serrations and large spines; usually with sclerotized acute anterolateral spines or projections (Figs. 1–4).

Female imago.—Body length 9–17 mm, forewing 10–16 mm. Similar maculation as male. Legs colored as male. Subanal plate with no or only a slight broad posteromedian emargination (Fig. 6). Caudal filaments as male.

Egg.—Biconvex with knob-terminated coiled threads closely spaced at center of one side (Figs. 17–20).

Nymph.—Posterior gills without stout sclerotized spines on apical margin (Fig. 7). Single gill at base of each forecoxa, except *I. sayi* with many gill filaments forming a tuft. Middorsal abdominal stripe present or absent.

Etymology.—Feminine; Greek adjective, *Prionoides*, “appearing like a saw,” referring to the penial lobes with dorsal incurved flap with sawlike marginal serrations.

Geographic range.—Eastern United States from Maine south to Georgia, except *I. sayi* which occurs from Montana southeast to Illinois, Missouri, Arkansas, Mississippi, and Florida.

Species included.—*Isonychia annulata* Traver, *I. aurea* Traver, *I. georgiae* McDunnough, *I. notata* Traver, *I. obscura* Traver, *I. sayi* Burks, *I. serrata* Traver, *I. similis* Traver, and *I. thalia* Traver.

Discussion.—Male and female imagoes are easily distinguished from *Isonychia* s.s. by: (1) Subgenital plate broadly concave or slightly emarginate; (2) penes armed dorsally; (3) subanal plate with no or only a slight broad posteromedian emargination; (4) biconvex eggs; and (5) usually conspicuous dorsal abdominal color patterns. Mature nymphs may be readily separated by the lack of spines on the apical margin of the posterior gills (Fig. 7) and usually possessing a single gill at the base of each forecoxa (except *I. sayi*).

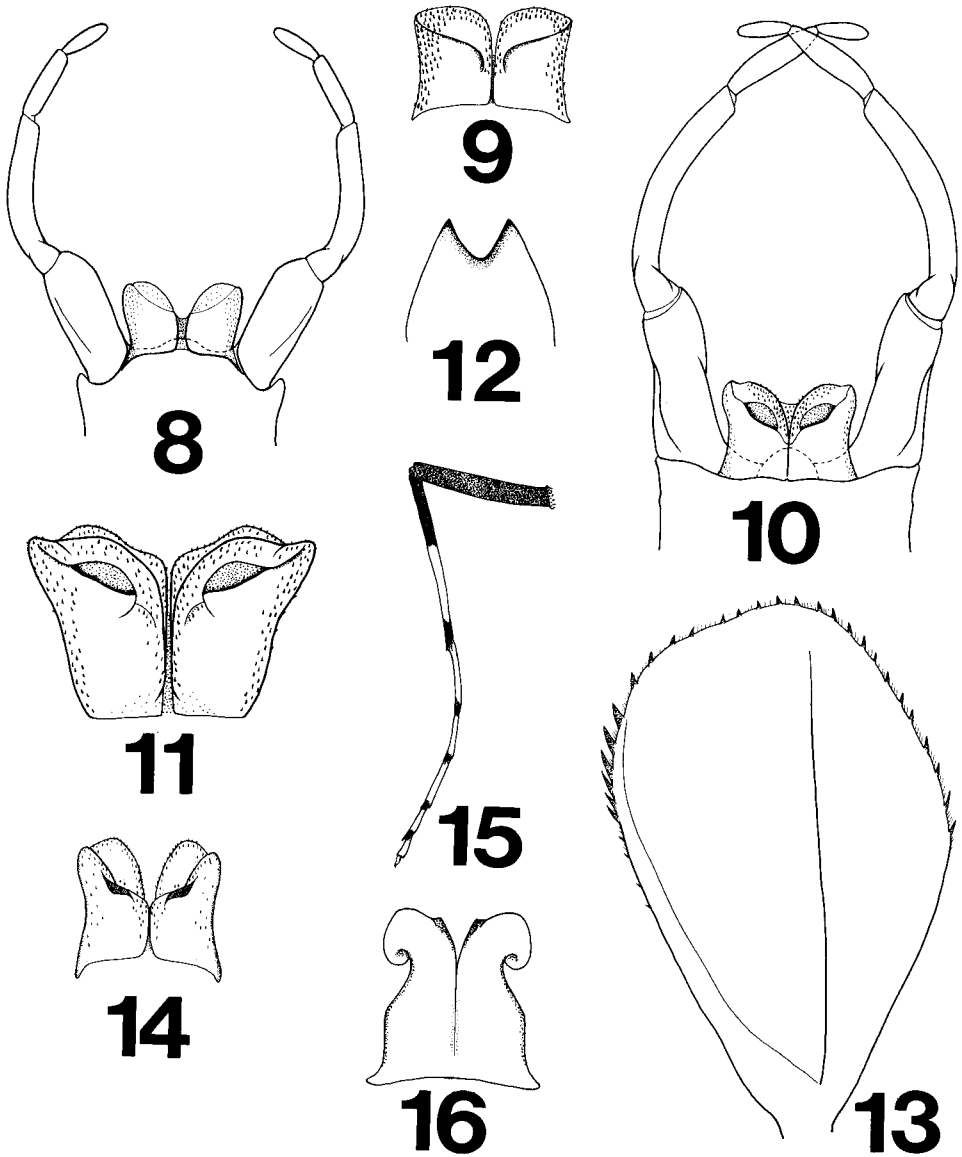
There are two general shapes of penes in *Prionoides*. *Isonychia annulata*, *georgiae*, *notata*, *obscura*, *sayi*, *serrata*, and *thalia* have acute apical lateral projections which are usually toothed (Figs. 1–4). *Isonychia aurea* and *similis* have toothed rounded anterolateral margins instead of the acute lateral projections (Fig. 5).

Subgenus *Isonychia* Eaton, *sensu stricto*

Isonychia Eaton, 1871: 33, 134. Type-species: *I. manca* Eaton. Original designation.

Male and female imagoes of *Isonychia* s.s. are distinguished from *Prionoides* by: (1) Deeply excavated subgenital plate; (2) penes without incurved and serrated medial flap; (3) subanal plate moderately to deeply emarginate; and (4) eggs spherical to subspherical. Mature nymphs possess stout spines on apical margin of all gills (Fig. 13), and gills in tufts at bases of forecoxae.

Isonychia s.s. may be readily divided into four species groups based on male imago penes form. No reliable morphological characters have been found to separate all the female imagoes and nymphs to species group.



Figs. 8–16. *Isonychia* (*Isonychia*). 8–11, 14, 16, Male genitalia, dorsal. 8, *I. campestris* (*sicca* group). 9, *I. sicca* (*sicca* group). 10, *I. tusculanensis* (*bicolor* group). 11, *I. bicolor* (*bicolor* group). 12, Subanal plate (*bicolor* group). 13, 7th nymphal gill (*bicolor* group). 14, *I. arida* (*arida* group). 15, Male foreleg (*arida* group). 16, *I. diversa* (*diversa* group).

Sicca Group

Male imago.—Body length 8–16 mm, forewing 9–15 mm. General body color reddish brown to dark red; posterior margins of terga purplish black or dark brown, sometimes with indistinct whitish middorsal stripe with bordering submedian streaks. *Isonychia intermedia* with abdomen reddish purple with yellowish-white maculae. Wings hyaline, veins and crossveins brown to black, sometimes

appearing tinged with light brown; stigmatic area whitish opaque, Prothoracic leg with tarsal ratio 0.76–1.15; femur reddish brown to brownish yellow; tibia brown to yellowish brown, usually darker brown basally and apically; tarsus yellowish with segments tinged with brown. Meso- and metathoracic legs yellowish to white with tarsal segments usually tinged with red or gray. Caudal filaments yellowish to whitish with brown articulations near bases, but occasionally marking entire filament.

Male genitalia.—Subgenital plate with a deep posteromedian emargination, with broadly rounded posterior medial dome (Fig. 8). Forceps 4-segmented sometimes appearing 5-segmented; segment 1, $\frac{3}{5}$ – $\frac{3}{4}$ length of segment 2. Penes with ventral lobe very broadly rounded or subtruncate; dorsal lobe without flap or roll, at most with a slightly sclerotized median margin (Figs. 8–9). Both ventral and dorsal lobe with minute surface spines. Penes length $\frac{2}{3}$ – $\frac{4}{5}$ of width.

Female imago.—Body length 9–16 mm, forewing 9–15 mm. Similar maculation as male. Legs colored as male. Subanal plate with deep posteromedian notch (as Fig. 12). Caudal filaments same as male.

Egg.—Spherical with knob-terminated coiled threads covering entire egg or more densely packed on one hemisphere (Figs. 27–28).

Nymph.—Posterior gills with stout sclerotized spines on apical margins (Fig. 13). Forecoxal gills in tufts. Middorsal abdominal stripe present.

Geographic range.—Western, midwestern, and southern United States. Central Canada, Mexico, and Mesoamerica.

Species included.—*Isonychia campestris* McDunnough, *I. intermedia* (Eaton), *I. manca* Eaton, *I. sicca* (Walsh).

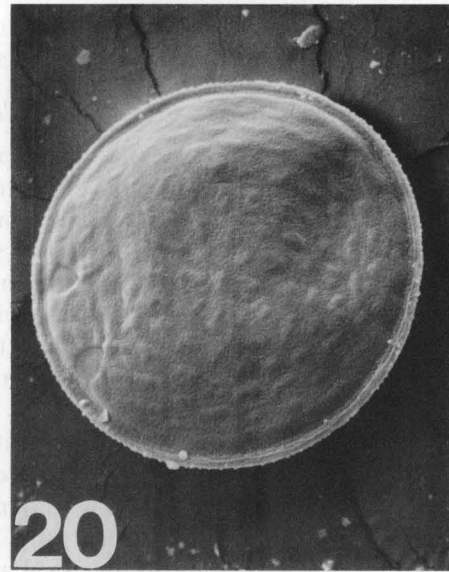
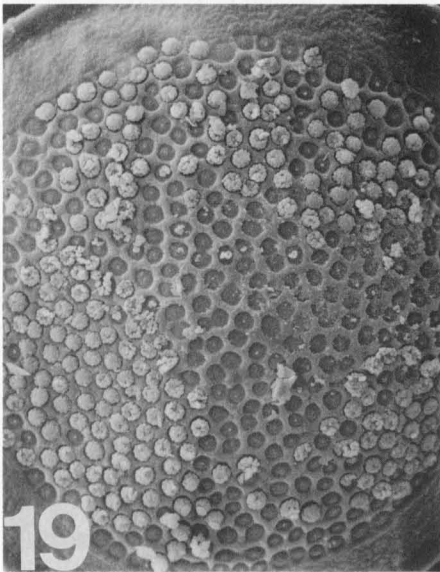
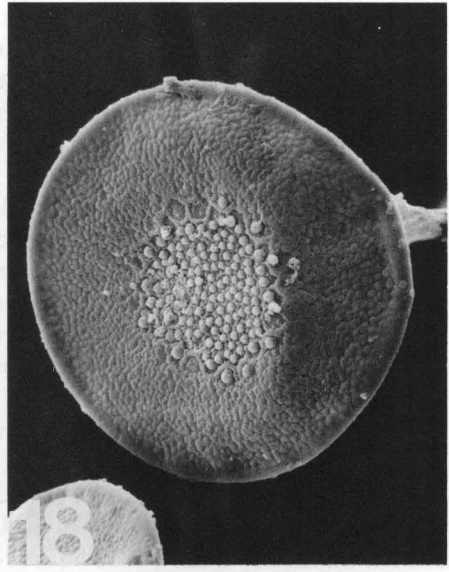
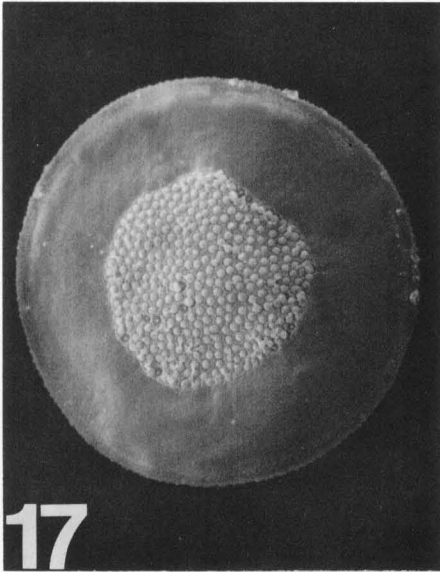
The Pakistan species, *I. khyberensis* (Ali) may belong here.

Discussion.—The relative simple and short penes readily distinguish this species group. The nymphs are very similar to the other species groups of *Isonychia* s.s. and cannot be distinguished presently except by geography. There is apparently an undescribed species from Mexico and Honduras.

Bicolor Group

Male imago.—Body length 9–16 mm, forewing 9–16 mm. General body color yellowish red to dark red; posterior margins of abdominal terga black, sometimes with indistinct whitish middorsal stripe; additional dark middorsal, submedian, and lateral maculae present in *I. velma*. Wings variable; usually ranging from hyaline with veins and crossveins whitish and stigmatic area whitish opaque, to veins and crossveins reddish brown with stigmatic area tinged with reddish brown; *I. tusculanensis* has distal $\frac{1}{3}$ of forewing brown and *I. velma* has outer margin of hindwing tinged with red. Prothoracic leg with tarsal ratio .79–.95; femur light to dark brown; tibia ranging from whitish to brownish. Meso- and metathoracic legs whitish to yellowish, sometimes tibia, tarsi and claws tinged with red or gray. Caudal filaments vary from whitish to yellowish without dark articulations except for a few basal segments to completely reddish with articulation darker or lighter in color.

Male genitalia.—Subgenital plate with deep posteromedian emargination; with broadly rounded posterior medial dome (Fig. 10). Forceps 4-segmented, sometimes appearing 5-segmented; segment 1, $\frac{2}{3}$ – $\frac{1}{2}$ length of segment 2. Penes with anterior margin of ventral lobe usually undulate; apices of dorsal lobes somewhat



Figs. 17–20. *Isonychia* (*Prionoides*), eggs. 17, *I. georgiae*, side with knob-terminated coiled threads, 380 \times . 18, *I. sayi*, side with knob-terminated coiled threads, 350 \times . 19, *I. annulata*, details of knob-terminated coiled threads, 550 \times . 20, *I. georgiae*, side without knob-terminated coiled threads showing chorionic tageniform micropyles, 280 \times .

divergent, each dorsal lobe with a prominent slightly sclerotized flap or roll on medial edge (Figs. 10–11). Both ventral and dorsal lobe with minute surface spines. Penes length $\frac{3}{4}$ to subequal as wide.

Female imago.—Body length 9–16 mm, forewing 9–16 mm. Similar maculation

as male. Legs colored as male. Subanal plate with moderate to deep posteromedian emargination (Fig. 12). Caudal filaments as male.

Egg.—Spherical to slightly flattened at poles with knob-terminated coiled threads closely spaced in a uniform layer covering entire egg or with some areas slightly more dense than others (Figs. 21–24).

Nymph.—Posterior gills with stout sclerotized spines on apical margin (Fig. 13). Forecoxal gills in tufts. Middorsal abdominal stripe present or absent.

Geographic range.—Eastern and midwestern North America with only one far western species (*I. velma*) from northern California and Oregon.

Species included.—*Isonychia bicolor* (Walker) = (*albomanicata* Needham), *I. christina* Traver, *I. circe* Traver, *I. fattigi* Traver, *I. harperi* Traver, *I. matilda* Traver, *I. pacoleta* Traver, *I. rufa* McDunnough, *I. sadleri* Traver, *I. tusculanensis* Berner, and *I. velma* Needham.

Tentatively most of the other Palearctic and Oriental *Isonychia* may be placed here: *I. formosana* (Ulmer), Formosa; *I. grandis* (Ulmer), Java and Sumatra; *I. ignota* (Walker), Eurasia; *I. japonica* (Ulmer), Japan and Eastern Asia; *I. kiangsiensis* Hsu, China; *I. polita* Bajkova, USSR; *I. sumatrana* (Navas)?, Sumatra; *I. ussurica* Bajkova, USSR; *I. validus* (Navas)?, Japan; *I. winkleri* Ulmer, Borneo.

Discussion.—This large homogenous group of species may be distinguished in the male imago by the characteristic genitalia. Females cannot be readily separated from the *sicca* group without associated males. Within the *bicolor* group most Nearctic species are very similar and are very difficult to distinguish.

Arida Group

Male imago.—Body length 8–14 mm, forewing 8–13 mm. General body color light red to reddish brown; posterior margins of abdominal terga purplish black; usually with indistinct whitish middorsal stripe with submedian streaks. Wings hyaline, veins and crossveins whitish, stigmatic area whitish opaque. Prothoracic leg with tarsal ratio .70–.95; femur brown, sometimes darker apically, usually margined with black apically; tibia bicolored (Fig. 15), whitish medially, dark brown at base and tip. Meso- and metathoracic legs yellowish. Caudal filaments whitish to yellowish without dark articulations, occasionally several basal segments faintly marked with brown.

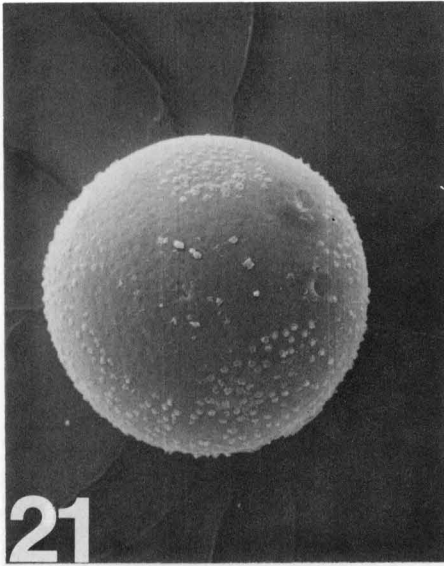
Male genitalia.—Subgenital plate with deep posteromedian emargination; with rounded medial posterior dome. Forceps 4-segmented, with segment 1 subequal to length of segment 2. Penes with ventral lobe broadly rounded apically, dorsal lobes narrowly rounded apically (Fig. 14). Each dorsal lobe with a small medial slightly sclerotized roll. Both ventral and dorsal lobes with minute spines. Penes usually as wide as long.

Female imago.—Body length 11–16.5 mm, forewing 11–16 mm. Similar maculation as male. Legs colored as male. Subanal plate with a moderate to deep median notch as Fig. 12. Caudal filaments as male.

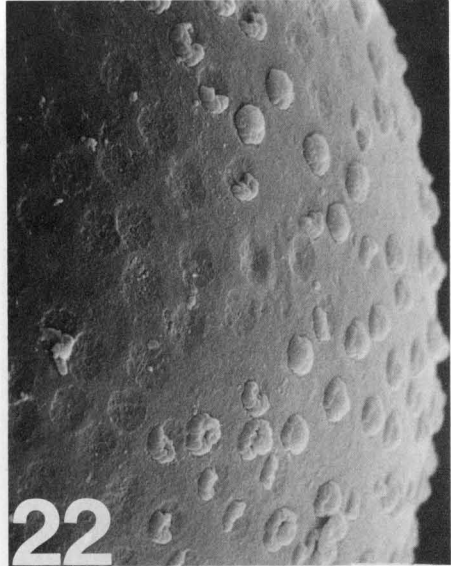
Egg.—Spherical, chorion smooth, with knob-terminated coiled threads spaced uniformly on surface; knob-terminated coiled threads with prominent distinct triangular knobs (Figs. 25–26).

Nymph.—Posterior gills with stout sclerotized spines on apical margins (Fig. 13). Forecoxal gills in tufts. Middorsal abdominal stripe present or absent.

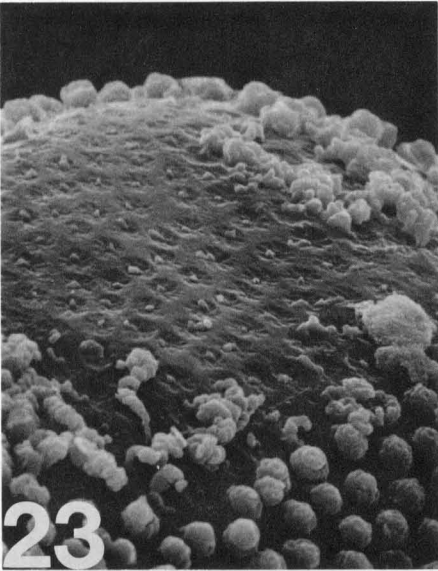
Geographic range.—Virginia south to Florida, west to Mississippi and Illinois.



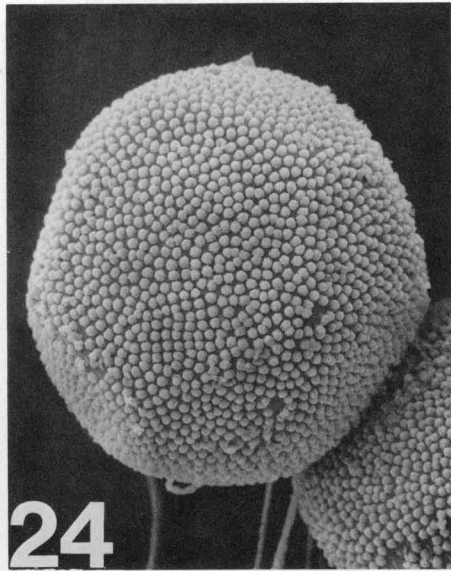
21



22



23

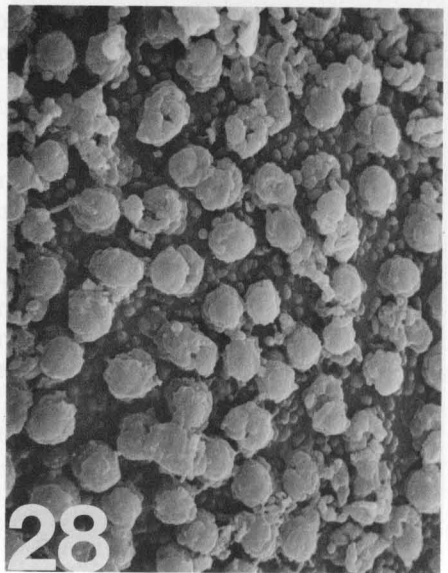
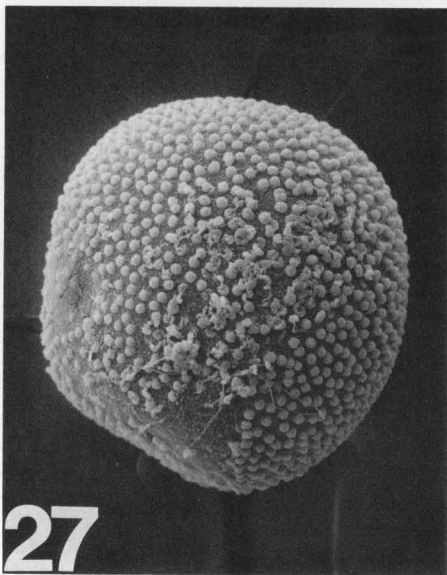
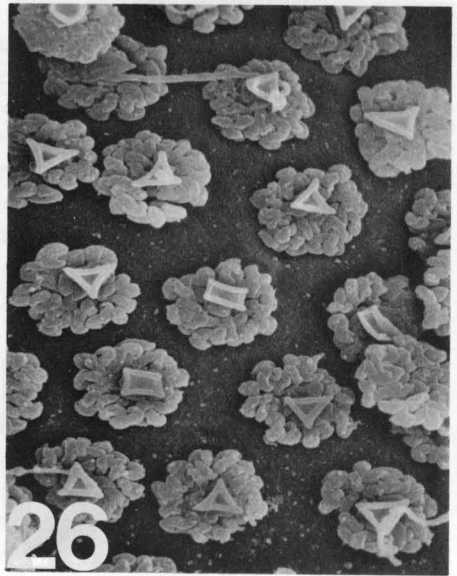
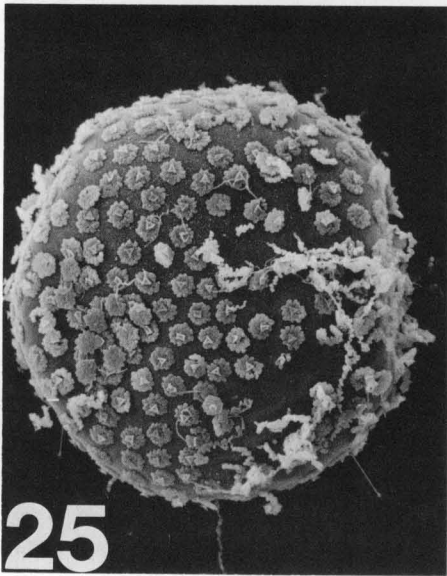


24

Figs. 21–24. *Isonychia* (*Isonychia*), eggs of *bicolor* group. 21, *I. bicolor*, 375 \times . 22, *I. bicolor*, details of knob-terminated coiled threads, 2000 \times . 23, *I. rufa*, details of knob-terminated coiled threads, 2000 \times . 24, *I. bicolor*, showing variation of density of knob-terminated coiled threads, 500 \times .

Species included.—*Isonychia arida* (Say) s.s. Burks, 1953, =*Isonychia pictipes* Traver, **NEW SYNONYMY**.

Discussion.—This species may be distinguished by the prominent bicolored foretibiae, males penes, and unusual eggs. The nymphs are similar to the *bicolor* and *sicca* groups and cannot be presently separated.



Figs. 25–28. *Isonychia* (*Isonychia*), eggs. 25, *I. arida* (*arida* group), 500 \times . 26, *I. arida*, details of knob-terminated coiled threads, 2000 \times . 27, *I. sicca* (*sicca* group), 500 \times . 28, *I. sicca*, details of knob-terminated coiled threads, 2000 \times .

The authors are in agreement with Burks (1953) on the identity of the true *arida* Say, and it is the same as *pictipes* Traver in all particulars.

Diversa Group

Male imago.—Body length 9 mm, forewing 9 mm. General body color brown to reddish brown; posterior margins of terga dark brown with whitish middorsal

stripe and submedian dark brown streaks. Wings hyaline, veins and crossveins whitish. Prothoracic leg with tarsal ratio of .73; femur dark red, black at apex; tibia blackish; tarsus light reddish brown. Meta- and mesothoracic legs whitish, femora tinged with red. Caudal filaments whitish without dark articulations.

Male genitalia.—Subgenital plate with a deep posteromedian emargination, with a broadly rounded medial posterior dome. Forceps 4-segmented; segment 1, $\frac{3}{4}$ as long as segment 2. Base of penes broad, constricted at about $\frac{3}{4}$ of length, with posterolateral margins of dorsal lobes rounded giving penes a mushroom-like appearance (Fig. 16).

Female imago.—Unknown.

Egg.—Unknown.

Nymph.—Unknown.

Geographic range.—Tennessee.

Species included.—*Isonychia diversa* Traver.

Discussion.—The “mushroom-like” penes readily distinguishes *I. diversa* males from the other groups of *Isonychia* s.s. 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 at the type-locality about three weeks later, but Traver (1934) did not include it as a paratype nor did she include a female imago also from the same locality and time. This badly damaged female imago is not described above since there is no positive association. The subanal plate of this specimen is similar to the *sicca* and *bicolor* groups.

KEY TO THE SUBGENERA AND SPECIES GROUPS

MALE IMAGOS

- 1. Subgenital plate broadly concave or with only slight posteromedian emargination (Fig. 1); penes dorsally with acute sclerotized lateral and marginal serrations and large spines on incurved flap (Figs. 1–5) *Prionoides*, new subgenus
- Subgenital plate with deep posteromedian emargination (Figs. 8, 10); penes dorsally without incurved flap bearing sclerotized teeth or serrations (Figs. 8, 9, 10, 11, 14, 16); subgenus *Isonychia* 2
- 2. Penes mushroom-like (Fig. 16) *diversa* group
- Penes not mushroom-like (Figs. 8, 9, 10, 11, 14) 3
- 3. Foretibia white, dark brown at base and at apex (Fig. 15); penes as Fig. 14 *arida* group
- Foretibia entirely brownish, sometimes darker brown at base and apex; penes as Figs. 8 and 11 4
- 4. Penes with prominent lightly sclerotized dorsal flap or roll at medial edge; ventral lobe with posterior margin usually undulate (Figs. 10–11) *bicolor* group
- Penes without prominent lightly sclerotized dorsal flap or roll at medial edge, at most with only a slightly sclerotized medial margin; ventral lobe, usually very broadly rounded or subtruncate posteriorly (Figs. 8–9) *sicca* group

FEMALE IMAGOS

- 1. Subanal plate with no or only slight broad posteromedian emargination (Fig. 6) *Prionoides*, new subgenus

- Subanal plate with a moderate to deep posteromedian emargination (Fig. 12) subgenus *Isonychia*

MATURE NYMPHS

1. Posterior gills without apical stout marginal spines (Fig. 7); usually 2 diffuse dark spots in outer margin of each gill; forecoxae gills single (except *I. sayi*) *Prionoides*, new subgenus
- Posterior gills with apical stout marginal spines (Fig. 13); usually diffuse dark spots lacking in outer margin of each gill; forecoxae gills in tufts subgenus *Isonychia*

ACKNOWLEDGMENTS

We thank L. L. Pechuman, Cornell University, Ithaca, New York; J. D. Unzicker, Illinois Natural History Survey, Champaign; J. E. H. Martin, Biosystematics Research Institute, Agriculture Canada, Ottawa; L. Berner, University of Florida, Gainesville; G. F. Edmunds, Jr., University of Utah, Salt Lake City; W. L. Peters, R. W. Flowers, P. M. Grant, and H. M. Savage, Florida A&M University, Tallahassee; P. M. Liechti, State Biological Survey of Kansas; and R. S. Demaray, Nova Scotia, for the loan of specimens used in this study. Thomas O. MacAdoo, Department of Foreign Languages, VPI&SU, Blacksburg, verified the etymology of *Prionoides*.

LITERATURE CITED

- Burks, B. D. 1953. The mayflies or Ephemeroptera of Illinois. Bull. Ill. Nat. Hist. Surv. 26: 1-216.
- Eaton, A. E. 1871. A monograph on the Ephemeridae. Trans. Entomol. Soc. Lond. 19: 1-164.
- Edmunds, G. F., Jr. 1962. The principles applied in determining the hierarchic level of the higher categories of Ephemeroptera. Syst. Zool. 11: 22-31.
- Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis. 330 pp.
- Kopelke, J. P. and I. Müller-Liebenau. 1981. Eistrukturen bei Ephemeroptera und deren Bedeutung für die Aufstellung von Artengruppen am Beispiel der europäischen Arten der Gattung *Baetis* Leach, 1815. Tiel. III: *buceratus*-, *atrebatinus*-, *gracilis*- und *muticus*- Gruppe (Ephemeroptera: Baetidae). Dtsch. Entomol. Z. (N. F.) 28: 1-6, Tafel 1-7.
- Koss, R. W. and G. F. Edmunds, Jr. 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zool. J. Linn. Soc. 55: 267-349.
- McDunnough, J. 1931. The genus *Isonychia* (Ephemeroptera). Can. Entomol. 63: 157-163.
- Traver, J. R. 1932. Mayflies of North Carolina. J. Elisha Mitchell Sci. Soc. 47: 163-236.
- . 1934. New North American species of mayflies (Ephemerida). J. Elisha Mitchell Sci. Soc. 50: 189-254.
- . 1935. In Needham, J. G., J. R. Traver, and Y. C. Hsu. The biology of mayflies with a systematic account of North American Species. Comstock, Ithaca, N.Y. 759 pp.