THE MAYFLY FAMILY BAETISCIDAE
(EPHEMEROPTERA). PART II BIOSYSTEMATICS
OF THE GENUS BAETISCA

MANUEL L. PESCADOR
Laboratory of Aquatic Entomology
Florida A and M University
Tallahassee, Florida 32307

LEWIS BERNER
Department of Zoology
University of Florida
Gainesville, Florida 32611

INTRODUCTION

The taxonomy, phylogeny, ecology, and life histories of the genus *Baetisca*, the only member of the family Baetiscidae, was reviewed in Part I of this treatment in 1980 (Berner and Pescador). This section completes our examination of the subject and includes a few changes in our earlier ideas about relationships which we believed existed when Part I was written.

After much careful study of all available material, we have decided to provide as full a treatment of each species as possible. Descriptions are given for last instar nymphs and for male and female adults. We considered seriously including descriptions of the subimaginal stage as well, especially as we earlier felt that there were specific differences in wing patterns; however, after due consideration, we have concluded that the patterns are not sufficiently distinctive to warrant their use for separating the species.

We are indebted to many people and institutions for their kind assistance and interest in this project. Dr. William L. Peters has

---

1This research was supported in part by a grant (FLAX 79009) from SEA/CR, USDA.
been most generous in allowing us access to all *Baetisca* specimens in the collections of Florida A & M University and he has provided help in many other ways. Other persons and institutions who have cooperated fully by lending us specimens and providing data include Richard K. Allen, Huntington Beach, California; David R. Barton, University of Waterloo; Ross T. Bell, University of Vermont; George F. Byers, University of Kansas; The Canadian National Collection of Insects, Arachnids, and Nematodes; Paul H. Carlson, South Carolina Department of Health and Environmental Control; Hugh F. Clifford, University of Alberta; R.S. Demaray, Lower Sackville, Nova Scotia; D.L. Deonier, Miami University; Richard M. Duchrow, Missouri Department of Conservation; George F. Edmunds, University of Utah; David Et nier, University of Tennessee; John F. Flannagan, Freshwater Institute, Winnipeg; Museum of Comparative Biology, Harvard University; K. Elizabeth Gibbs, University of Maine; George L. Harp, Arkansas State University; W.L. Hilsenhoff, University of Wisconsin; Marjorie Hughes, Manitoba Department of Mines, Winnipeg; The Illinois Natural History Survey, Urbana; Boris Kondratieff, Virginia Polytechnic Institute and State University; Thomas M. Lager, Institute of Paper Chemistry, Appleton, Wisconsin; Paul M. Liechti, State Biological Survey of Kansas; Jerry A. Louton, University of Tennessee; W.P. McCafferty, Purdue University; Museum of Zoology, University of Michigan; Department of Entomology, University of Minnesota; Robert E. Moase, Pennsylvania Fish Commission; Robert Newell, Stearns-Roger, Inc., Denver; Jane A. Schafrik, Cornell University; Bill Stark, Mississippi College; Bernard Sweeney, Stroud Water Research Center; Donald Tarter, Marshall University; Kenneth J. Tennesen, Tennessee Valley Authority; J. Reese Voshell, Virginia Polytechnic Institute and State University; Tina White, Clemson University.

Original illustrations for this paper have been prepared mostly by Esta Belcher, Staff Artist, Department of Zoology, University of Florida; and Janice G. Peters, Laboratory of Aquatic Entomology, Florida A & M University.
Figure 1. Lateral view of male imago of *Baetisca rogersi* Berner (after Pescador and Peters, 1974).

TRANS. AMER. ENT. SOC., VOL. 107
MAYFLY FAMILY BAETISCIIDAE

METHODS AND MATERIALS

In addition to the *Baetisca* specimens we collected and those we reared in the field and laboratory, several other collections were also made available for study. Cooperating individuals and organizations are listed above.

The technique described by Towns and Peters (1978) was followed in preparing the specimens for SEM observation. All measurements were made using a calibrated ocular micrometer and they are given to the nearest 0.5 mm. The relative length of each of the segments of the foreleg of the male imago of the genus was compared to the length of the fore tibia and is expressed as a ratio. These are average ratios based on male specimens of all species of the genus. The ratio of length to width of the nymphal mesonotal shield was obtained by measurement of the maximum length as related to the width at the base of the lateral spines.

Localities, stages (N for nymph; A for adult, which includes both imago and subimago), and deposition of examined specimens are given in the treatment of each species to facilitate access to specimens for future reference. Abbreviations for depositories are as follows: California Academy of Sciences (CAS), Clemson University (CLU), Cornell University (CU), Canadian National Collections (CNC), Florida A & M University (FAMU), Florida State Collection of Arthropods (FSCA), Harvard University (HU), Illinois Natural History Survey (INHS), State Biological Survey of Kansas (SBSK), University of Florida (UF), University of Michigan (UMich), University of Minnesota (UMinn), University of Tennessee (UT), University of Utah (UU), University of Wisconsin (UW), and Virginia Polytechnic Institute and State University (VPISU).

Genus *Baetisca* Walsh

Figure 1


Imago. Length. — male body 5.0-11.7 mm, forewing 6.0-12.8 mm; female body 5.5-12.3 mm, forewing 7.0-16.1 mm.

Head. — Posterior margin slightly emarginate at median line. Male eyes large, almost contiguous to contiguous dorsally, posteriorly projected almost covering pronotum. Female eyes small, separated on meson of head by a distance equal to twice the width of an eye.
Thorax. — Pro- and metathorax reduced; mesothorax robust with well-developed scutellum extended beyond posterior margin of metanotum. Prosternum with 2 prominent spinous projections between fore coxae.

Wings. — Membrane of fore- and hind wing hyaline or flushed with ruby or orange to reddish-brown; maximum width of forewings approximately 1/3 the maximum length; outer margin slightly scalloped; veins CuA and CuP parallel at base, slightly divergent distally; vein A₅ terminates in outer margin of wings, veins A₇ and A₈ short, end distally near base of wing; cubital intercalaries absent. Hind wing almost circular with blunt costal projection near base; length approximately 1/3 of forewing, maximum width approximately 5/6 the maximum length; basal 1/2 with numerous crossveins; long intercalaries present.

Legs. — Male: Foreleg almost as long as body; ratio of segments to that of tibia (approximately) — femur = 1.34, tibia = 1.00, tarsal segments 1 = 0.72, 2 = 0.43, 3 = 0.41, 4 = 0.33, 5 = 0.22; fore tarsal claws similar, blunt; meso- and metatarsal claws dissimilar, one hooked, the other blunt. Tarsal segment 1 of meso- and metathoracic legs fused with tibia and subequal to length of segment 5. Female; Foreleg approximately 1/2 length of body; fore, meso-, and metatarsal claws dissimilar, one hooked, the other blunt.

Abdomen. — Short and chunky, sharply tapered distally; segments 2-5 short, of subequal length; tergite 6 with weakly developed middorsal transverse elevation usually with network of fine black linings. Male genitalia (fig. 2e): genital forceps 2-segmented with segment 1 indented giving appearance of segmentation, prominent median knob on inner margin; basal 1/2 of inner margin crenulate with minute hairs, apical 1/2 including entire margin of 2 with short, peg-like setae; segment 2 approximately 1/6 length of segment 1. Penes sharply (fig. 2g) to gradually tapered apically (fig. 2h-]), base sharply (fig. 2j) to gradually enlarged (fig. 2j); penes with prominent subapical process. Female sternite 9 deeply cleft apically. Cerci slightly shorter than body length, median filament rudimentary, unsegmented.

Subimaggo. — Wing membranes brown-checkered with numerous white spots of various sizes and patterns (fig. 3e, f).

Egg. — Oval; polar cap present; chorion with pronounced ridges and minute fiber coils (figs. 3a-d).

Mature nymph. — Length: body 6.0-13.9 mm; caudal filaments 1.8-3.5 mm.

Head: Hypognathous; gena flared and rounded (fig. 13b) or angulate (fig. 10b) to spinous (fig. 10d). Antennae 7-10 segmented. Mouthparts as illustrated (figs. 5a-f). Labrum rectangular, length approximately 1/2 maximum width; prominent dorsal tubercles and thick marginal spinous hairs present. Mandibles with almost straight outer lateral margin and with prominent dorsal tubercles; short prosthecæ with hair tuft, and sclerotized knob-like projection below molar area. Maxillae with long, sinuous cardo; palpi 3-segmented with segment 1 shortest, segments 2 and 3 of subequal length; galea-lacinia with both slender and broad long spinous apical crown. Lingua of hypopharynx oval and broad with short spinous apical hairs, superlingua with moderately long apical hairs. Labial submentum greatly expanded laterally, palpi 3-segmented, segment 1 slightly longer than segment 2, inner apical corner of segment 2 with finger-like projection which forms pincer-like structure with short segment 3; glossae twice as broad as paraglossae.

TRANS. AMER. ENT. SOC., VOL. 107
**Thorax:** Pronotum narrow, fused with massive mesonotal shield which covers metanotum and abdominal tergites 1-5 and basal 1/2 of tergite 6. Prosternum narrow and prominently indented; meso- and metanotum fused. Legs short; fore coxae with stubby basal spine fitted in prosternal indentation; femoral venter with prominent tubercles with hairs (fig. 8a); tibiae short, approximately 2/3 length of tarsi; tarsal claws slender, non-denticulate (fig. 5g).

**Abdomen:** Gills on segments 1-6 (figs. 6a-f); gill 1 with long pointed dorsal lamella and enormous fibrilliform portion consisting of ramified tracheal branches; gill 2 greatly flattened and expanded covering gills 3, 4, and 5; gills 3 structurally similar to gill 1, except smaller and dorsal lamella is not as pointed; gills 4 and 5 with blunt lamella and reduced fibrilliform portion; gill 6 reduced, oval with transparent apical 1/2 and fitted exactly into dorsal concavity of pyramidal structure on tergite 6. Prominent black spot near base of gills 2-5, largest on tergite 2; tergite 6 with prominent truncated pyramidal structure (fig. 4b); tergites 7-10 and posterior 1/2 of tergite 6 with prominent tubercles (fig. 8e). Sternites 2-5 of subequal length; sternite 6 longer than those anterior to it. Posterior projections on segments 6-9. Caudal filaments: cerci and median filament subequal length with thick ventrolateral hairs except at extreme base (fig. 8f).

**Subgenus Fascioculus** Pescador and Berner, new subgenus

**Imago.** — **Length:** Male body 9.5-10.0 mm, forewing 8.0-10.0 mm; female body 9.0-11.0 mm, forewing 10.0-12.0 mm.

**Head:** Eyes striped vertically with alternate light and dark bands.

**Thorax:** Forewings flushed throughout with ruby color.

**Abdomen:** Penes sharply tapered near apex (fig. 2g).

**Nymph.** — **Length:** body 10.0-13.0 mm, caudal filaments 2.0-3.0 mm.

**Head:** Lateral and anterior margins with long hairs (fig. 12b); frontal projection absent (fig. 12b). Eyes striped vertically with alternate light and dark bands.

**Thorax:** Mesonotal shield compressed dorsoventrally and with long, marginal hairs; lateral spines narrow, base almost linear throughout its entire length; deep and narrow notch near posterior margin of notal shield (fig. 12b). Sternae lack distinct markings.

**Legs:** Ventral surface of femora relatively smooth; weakly dentate, with long hairs arising on small tubercles (fig. 8b); tarsal claws slightly curved (fig. 12b) and more than 2/3 length of tibiae.

**Abdomen:** Long hairs on lateral margins; posterolateral projections on segments 6-9 outcurved (fig. 12b). Sternae lack distinct markings.

**Etymology:** fasci (L.) = a band; oculus (L.) = an eye.

**Type species:** *Baetisca escamibiensis* Berner.

**Discussion:** *Fascioculus* is monotypic and is known only from extreme northwestern Florida. The characters given above distinguish the subgenus from *Baetisca* s.s.
Subgenus *Baetisca* s.s. Walsh

**Imago.** — *Length:* Male body 5.0-11.7 mm; forewing 7.0-12.8 mm; female body 5.5-12.3 mm, forewing 7.0-15.6 mm.

**Head:** Eyes uniformly colored.

**Thorax:** Forewings hyaline to partly or entirely flushed with orange or reddish brown.

**Abdomen:** Penes gradually tapered apically (fig. 2e).

**Nymph.** — *Length:* body 6.0-13.9 mm; caudal filaments 1.8-3.0 mm.

**Head:** Margins glabrous or with few minute hairs on basal 1/3 of lateral margins; frontal projection present (fig. 4a). Eyes uniformly colored.

**Thorax:** Mesonotal shield strongly convex, marginally glabrous or with few minute hairs; base of lateral spines broad (fig. 4a); with or without broad and shallow median depression near posterior margin of mesonotal shield (fig. 4b). Sterna with distinct markings (fig. 13b).

**Legs:** Ventral surface of femora granulate (fig. 8a); cleft setae arising on prominent tubercles (fig. 8c); tarsal claws strongly curved (fig. 5g), less than 1/3 length of tibiae.

**Abdomen:** Lateral margins glabrous or with few minute hairs. Posterolateral projections on segments 6-9, incurved (fig. 4a). Sterna with distinct markings (fig. 13b).

**Type species:** *Baetisca obesa* (Say).

**Discussion:** *Baetisca* s.s. consists of eleven species which are widely distributed over most of eastern North America, into the Great Plains, and to the Northwest Territories of Canada. The characters given above distinguish it from the subgenus *Fasciocolus*.

**Key to Imagoes**

1 Penes sharply tapered distally (fig. 2g); eyes striped ................................................... subgenus *Fasciocolus*, *B. escambiensis* Berner

   Penes smoothly tapered distally (fig. 2h-j); eyes uniformly colored .................................. subgenus *Baetisca* s.s., 2

2(1) Wings fully or partially flushed with orange, yellowish, to reddish-brown

   (figs. 1, 2a, b) .......................................................................................................................... 3

   Wings hyaline, rarely with brown tint at extreme base ......................................................... 7

3(2) Abdominal tergite 10 with a pair of small dark-brown spots; basal 1/3 or less of hind wing faintly flushed with orange brown ................................................................. *B. becki* Schneider and Berner

   Abdominal tergite 10 lacks spots; basal 1/2 or entire hind wing flushed with orange, yellowish, to reddish-brown .............................................. 4

4(3) Basal 3/4 or less of hind wing flushed with reddish brown .............................................. 5

   Entire hind wing flushed with orange or yellowish-brown ................................................... 6

5(4) Basal 1/3 of forewing and basal 3/4 of hind wing strongly flushed with dark reddish-brown (fig. 2a, b); abdominal tergites 7-9 with transverse anterior marginal black band .................... *B. rogersi* Berner

**Trans. Amer. Ent. Soc., Vol. 107**
MAYFLY FAMILY BAETISCIDAE

Basal 1/2 of fore- and hind wings faintly flushed with reddish-brown; abdominal tergites 7-9 lack anterior marginal banding................. B. carolina Traver

6(4) Penes lanceolate, gradually enlarged basally (fig. 2i); basal 1/3 of forewing and entire hind wing flushed with orange...... B. rubescens (Provancher)
Penes ovate, abruptly enlarged basally (fig. 2j); basal 1/3 of forewing and entire hind wing faintly flushed with yellowish-brown................. B. berneri Tarter & Kirchner

7(2) Penes lanceolate, apically blunt (fig. 2i)........................................ B. obesa (Say)
Penes deltoid, apically pointed (fig. 2h).................................................. 8

8(7) Abdominal sternae dark brown, posterior margin of sternites 6-8 almost black; sternae with broad, brownish, elongate, anterolateral markings................................................................. B. gibbera Berner
Abdominal sternae pale to light brown; markings absent ........................................... 9

9(8) Longitudinal veins of forewing brown ............... B. laurentina McDunnough
Longitudinal veins of forewing pale, vein C, Sc, and R pale to light brown...................... B. lacustris McDunnough

KEY TO MATURE NYMPHS

1 Eyes striped; abdominal segments 6-9 with long, thick, lateral hairs (fig. 12b), posterolateral projections outcurved (fig. 12b); tarsal claws more than 2/3 length of tibiae... subgenus Fasciocolus, B. escambiensis Berner
Eyes uniformly colored; abdominal segments 6-9 either glabrous or with few minute hairs (fig. 13); tarsal claws less than 2/3 length of tibiae........................................ Baetisca s.s., 2

2(1) Genal spines present (fig. 10c)................................................................. 3
Genal spines absent (fig. 10b)................................................................. 5

3(2) Lateral spines of mesonotal shield blunt (fig. 14a)....................................... B. rubescens (Provancher)
Lateral spines of mesonotal shield sharp pointed (fig. 11b)................. 4

4(3) Caudal filaments prominently banded with dark brown at base (fig. 10d).............. B. berneri Tarter & Kirchner
Caudal filaments unbanded (fig. 11b)......................................................... B. carolina Traver

5(2) Dorsal projections on mesonotal shield well developed, distinctly taller than medial hump (fig. 7e)................................................................. 6
Dorsal projections on mesonotal shield weakly to moderately developed, height less than, or subequal to, that of medial hump (fig. 7f).............. 8

6(5) Lateral spines prominent, long, sharp pointed (fig. 9a); thoracic and abdominal markings as in fig. 19a, b........................................ B. becki Schneider & Berner
Lateral spines shorter; thoracic and abdominal markings not as above (fig. 12a; 13c, d)............. 7

7(6) Frontal projection well developed, distinctly extended beyond anterior margin of head (fig. 12a); ventral margins of mesonotal shield lack dark-brown outline (fig. 13d); abdominal sternites 2-6 with prominent dark-brown spots near lateral margins...................... B. obesa (Say)
Figure 2. Adult male structures of Baetis: a. forewing; b. hind wing; c. tenth abdominal segment to show vestigial median filament; d-e. ventral view of genitalia; f. fore claw; g-j. penes. g. B. escamblensis; h. B. gibbera, lacustris, laurentina; i. B. becki, obesa, rogeri, rubescens; j. B. berner, carolina.
Frontal projection developed, not extended beyond anterior margin of head (fig. 13c); ventral margin of mesonotal shield prominently outlined with dark brown (fig. 13d); abdominal sternites 2-6 lack prominent dark-brown sublateral spots but freckled with brown (fig. 13d). ......................... B. laurentina McDunnough

Mesonotal shield strongly flared with lateral margins almost straight diagonally (fig. 11c); mesonotal shield length subequal to width, middorsal depression absent (fig. 4b); lateral spines of mesonotal shield as long as width at base ................................. B. gibbera Berner

Mesonotal shield weakly flared with lateral margins prominently curved near base of lateral spines (fig. 13a); mesonotal shield distinctly longer than width and middorsal depression present (fig. 4b); lateral spines of mesonotal shield more than 1-1/2 times as long as width at base .......... 9

Thoracic and abdominal sterna freckled with brown spots (fig. 13a, b); prominent brown spot on sternum medial to each coxa; margins of mesonotal spines weakly crenulate (fig. 13a); posteromedian elevation on abdominal tergites 7-9 weakly developed (fig. 4b) .................. B. lacustris McDunnough

Thoracic and abdominal sterna variable; lateral margins of mesonotal spines serrate (fig. 11a); posteromedian elevation on abdominal tergites 7-9 well developed (fig. 4b) ......................... B. rogersi Berner

**Baetisca (Baetisca) becki** Schneider and Berner

Figures 2i, 4a, 7e, 10a,b, 15c


**Male Imago** (in alcohol): — **Length:** body 6.2-6.8 mm; forewing 7.0-8.0 mm; caudal filaments 5.5-6.5 mm.

**Head:** Light brown. Scape and pedicel of antenna brown, flagellum yellowish. Eyes contiguous dorsally.


**Wings:** Longitudinal veins of fore- and hind wings light brown, base darker; crossveins colorless; membrane of fore- and hind wings hyaline, stigmatic area of forewing translucent white, basal 1/7 and costal membrane of forewings and basal 1/4 of hind wings faintly flushed with orange brown.

**Legs:** Yellowish; forelegs slightly darker; dorsum of tarsal claws light brown, venter pale yellow; light brown band on tarsal joints, more pronounced on meso- and metatarsi.
**Abdomen:** Terga orange brown, tergites 1-6 darker, remnants of gill attachments purplish-brown; interrupted median longitudinal dark-brown line on tergites 6-9; tergite 10 with a pair of small dark brown spots. Sterna pale yellowish. Genital forceps pale yellow, apex slightly darker; penes pale yellow, lanceolate, apically blunt and gradually enlarged basally (fig. 2i). Ceri yellow with light brown annulations at articulations; vestigial median filament pale yellow, reddish brown at extreme base.

**Female Imago** (in alcohol). — **Length:** body 6.0-7.0 mm; forewing 7.0-8.5 mm; caudal filaments 4.5-5.5 mm.

**Head:** Brown. Color of antenna as in male imago.

**Thorax:** Color and markings as in male imago except for being slightly paler.

**Wings:** Color of membrane and veins as in male imago.

**Abdomen:** Color and markings of terga and sterna as in male imago; sternite 9 shallowly cleft mid posteri orly, depth approximately 1/10 maximum width of sternite. Caudal filaments yellowish, base darker.

**Mature Nymph** (in alcohol). — **Length:** body 6.0-7.5 mm, caudal filaments 2.0-2.6 mm.

**Head:** Yellowish, dorsum mottled with reddish-brown. Frontal projection prominent, slightly bident. Genae strongly flared, broad and truncate (fig. 10b).

**Thorax:** Mesonotal shield relatively broad, ratio of length to width 1.3:1.0; prominent anterolateral lobe angular; lateromedial lobe broad, smoothly curved; lateral spines relatively long, approximately twice as long as width at base, sharp pointed; dorsal projections prominent, distinctly higher than medial hump; mesonotal shield yellow with brown mottling (fig. 4a, 10a); 6 conspicuous circular areas without mottling; lateral margins crenulate. Sterna yellowish; prosternum with 1 prominent dark-brown spot; meso- and metasterna with several dark-brown spots (fig. 10b).

**Legs:** Brownish-yellow; metastem with 2-3 dark-brown ventral spots, mesofemur with 1-2, and profemur with 0-1.

**Abdomen:** Tergites 5-6 with broad, dark-brown, dorsolateral mottling; tergites 7 and 9, and posterior 1/3 of tergite 6, with fine dark-brown mottling; narrow longitudinal dark-brown line on tergites 7-9, interrupted by posteromedian elevation. Sterna yellow with several large dark-brown spots, most numerous on sternite 6, least on sternite 9 (fig. 10b). Posterolateral projection on tergites 6-9 well developed, largest on tergite 9 (fig. 10a); posteromedian elevation on tergites 7-9 well developed, largest on 9 extending almost 1/3 length of tergite 10. Caudal filaments brownish-yellow.

**Variations:** Only slight color variation occurs among imagoes of *B. becki*. Few imagoes have the median areas of tergites much paler than lateral area, while others have a more or less uniform dark-brown abdominal terga. Whitish granulation on the head, thorax, and abdomen obfuscates the true body color of some female imagoes.

Nymphs of *B. becki* differ slightly in pigmentation. Some nymphs have few to several brown mottled areas on the ventral margins of the mesonotal shield while others lack pigmentation. Most nymphs have a linearly arranged transverse row of dark-brown spots on sternites 6-9 while others have spots scattered on most ster-
Figure 3.  *a-d.* SEM photographs of *B. rogersi* egg.  *a* and *c* to show polar cap;  
b. chorionic sculpturing;  
d. fiber coils on chorionic surface.  
*e* and *f.* Forewings of male subimagmo.  
*e. B. lacustris; f. B. rogersi.*
nites. Few nymphs have sternites 8 and 9 with 2 dark-brown spots or none on sternite 9; others, particularly the females, have both sternites with more than 2 spots.

**Geographical Distribution:** *Baetisca becki* is strictly a Coastal Plain species occurring in northwest Florida and south Alabama (fig. 15c).

**Discussion:** *B. becki* can be distinguished from the other species of the genus by the following combination of characters. In the imagoes; (1) basal 1/7 and costal membrane of forewings and basal 1/4 of hind wings are faintly flushed with orange-brown; (2) abdominal tergite 10 has a pair of small black spots; and (3) penes are lanceolate, apically blunt and gradually enlarged basally (fig. 2i). In the nymphs: (1) frontal projection is developed and slightly bifid (fig. 10a); (2) genae are greatly flared, broad and truncate (fig. 10b); (3) mesonotal shield has relatively long, laterally serrated, sharp-pointed spines (fig. 10a); (4) dorsal projections are prominent and spinous, distinctly higher than the medial hump (fig. 4a); and (5) thoracic and abdominal sterna have large, dark-brown spots (fig. 10b).

*Baetisca becki* appears to be most closely related to *B. rogersi* but can be distinguished from it by any of the following characters. In the imagoes: (1) male eyes are contiguous dorsally; (2) basal 1/7 and costal membrane of forewings and basal 1/4 of hind wings are faintly flushed with orange brown; and (3) abdominal tergite 10 has a pair of small black spots. In the nymph: (1) thoracic and abdominal sterna have several large dark-brown spots (fig. 10b); (2) lateral margins of mesonotal shield crenulate but not serrated (fig. 10a); and (3) dorsal projections of mesonotal shield are spinous and distinctly higher than the medial hump (fig. 4b).

**Biology and Ecology.** — Nymphs of *B. becki* are generally sympatric with *B. rogersi* except *becki* nymphs appear to be more abundant in swifter and deeper water with more shifting sand than *rogersi* nymphs living in the same river (Pescador and Peters, 1971; Berner and Pescador, 1980). Schneider and Berner (1963) collected nymphs in swiftly flowing sand-bottomed streams. Nymphs have been collected from September through May, and adults from February through May.

**Specimens Examined.** — **ALABAMA:** Clay Co: Cheaha Ck, 10 II 77 (N) (UT). Washington Co: 29 V 56 (N) (FSCA). FLORIDA: Okaloosa Co: Blackwater R, 4-1/2 mi NW Holt, 18 III 71 (N, A reared) (FAMU), 16 IV 71 (N) (FAMU), 23 IV 71 (A) (FAMU), 7, 8, 22, 27 IV 72 (N) (FAMU), 27 IV 73, 6 V 73 (N) (FAMU), 20-27
Figure 4.  a. Dorsal view of *B. becki* nymph to show structures; b. lateral view of *B. rogersi* nymph to show structures.
IV 74 (N) (FAMU), 5 V 74 (N) (FAMU), 24 V 74 (N, A reared) (FAMU), 28 III 75 (N) (FAMU), 5 I 77 (N) (FAMU), 5 II 77 (A) (FAMU), 5 IV 77 (A reared) (FAMU), 15-20 IV 77 (A) (FAMU), 28 IV 77 (A) (FAMU), Blackwater R, Bryant Bridge, 24 IV 70 (N) (FAMU), 9 V 70 (N, A reared) (FAMU), 20 II 71 (N) (FAMU), 26 IV 73 (N) (FAMU), Blackwater R, Kennedy Bridge, 26 IV 70 (N) (FAMU), 27-29 IV 72 (N, A reared) (FAMU), 2 V 73 (A) (FAMU), Blackwater R, 4-1/2 mi NW Cannon Town, 11-12 IX 68 (N) (FAMU), 16 IX 68 (N) (FAMU), 26-27 IV 69 (N) (FAMU), 21 II 71 (N) (FAMU), Blackwater R at Fla Hwy 4, 9 III 60 (N) (FAMU), Blackwater R 4 mi NW Baker, 13 III 71 (N) (FAMU), Ates Creek, 4 mi NW Holt, 16 IV 71 (N) (FAMU). Santa Rosa Co: Blackwater R, Riley Bluff, 11 II 72 (N) (FAMU), 8, 27 IV 72 (N) (FAMU), Sweetwater Creek, 9 III 60 (N) (UF).

**Baetisca (Baetisca) bremerei** Tarter and Kirchner

*Figures 2j, 9a, 10c,d, 15a*


**Male Imago** (in alcohol). — *Length:* body 9.5-9.8 mm; forewing 9.5-9.8 mm; caudal filaments 7.5-8.0 mm.

**Head:** Light brown, darker around bases of ocelli and antennae. Antennae light brown, progressively paler distally. Eyes almost contiguous dorsally.

**Thorax:** Pronotum yellowish with thin dark-brown marginal linings. Mesonotum yellowish, median longitudinal suture, parapsidal furrows, margins and apex of mesoscutellum yellowish medially with 2 small brown elevations. Metanotum brown. Sterna yellowish, pro- and metasterna paler and translucent.

**Wings:** Longitudinal veins of fore- and hind wings brown, slightly darker toward base; costal and subcostal veins of forewing with pale median interruptions; crossveins on basal 1/2 of fore- and hind wings light brown, remainder pale; stigmatic area opaque white; hind wings and basal 1/3 of forewings, including 2/3 of costal and subcostal membranes, faintly flushed with reddish-brown.

**Legs:** Light brown; coxae darker, tarsi and apical 2/3 of tibiae paler; meso- and metatarsal joints with narrow brown band; claws shiny brown.

**Abdomen:** Terga light brown, darker on tergites 1-6; remnants of gill attachments and posterior margins of tergites 4-8 purpulish-brown; pleural folds of tergites 1-6 with granular purplish-brown markings. Sterna brownish-yellow, posterior margins of sternites 4-5 and 7-8 purplish-brown; sternites 2-6 with prominent mediolateral black spots, greatly reduced on sternite 6. Genital forceps brownish-yellow, inner lateral margin paler, joints purplish-brown. Penes brownish-yellow, ovate, apically blunt and greatly enlarged basally (fig. 2j). Cerci yellowish; vestigial median filament yellowish to reddish-brown.

**Female Imago** (in alcohol). — *Length:* 9.0-11.0 mm; forewing 11.0-13.0 mm; caudal filaments 6.0-8.0 mm.

**Head:** Brownish-yellow, darker along margins. Color of antennae as in male imago.

**Thorax:** Pro- and mesonota greenish-yellow; median area of mesonotum, basal hump, and apex of mesoscutellum brown. Color and markings on remainder of nota.
including sterna as in male, except sternal intersegmental joints faintly washed with purplish-brown.

**Wings:** Color as in male imago.

**Legs:** Color as in male, except bandings on tarsal joints not as pronounced.

**Abdomen:** Color of terga as in male, markings not as pronounced; posterior margins of tergites 4-5 and 7 purplish-brown. Sterna pale yellow, markings as in male. Color of caudal filaments as in male.

**Mature Nymph (in alcohol).** — **Length:** body 7.5-11.5 mm; caudal filaments 2.0-3.0 mm.

**Head:** Brownish-yellow with few reddish-brown spots. Frontal projection weakly developed, truncate (fig. 10c). Genal spines well developed with upcurved brown tips, clearly visible when viewed dorsally (fig. 10c). Antennae yellowish, distal segments light brown.

**Thorax:** Mesonotal shield broad with ratio of length to width 1.15:1.00; anterolateral and lateromedial lobes weakly developed (fig. 4a); lateral spines short, length subequal to slightly longer than width at base (fig. 10c); dorsal projections weakly developed, distinctly lower than medial hump (fig. 4b); postero- median dorsal depression shallow and broad (fig. 4b). Mesonotal shield with small reddish-brown tubercles and linearly arranged reddish-brown mottling (fig. 10c); lateral margins finely crenulate. Sterna yellowish with reddish-brown tubercles.

**Legs:** Coxae brown, claws shiny brown, remainder of legs yellowish; femora with broad, dark-brown basal band and prominent black tubercles; tibiae and tarsi with prominent dark brown bands.

**Abdomen:** Tergites 7-9 and including posterior 1/3 of tergite 6 with dark brown spots similar to those in fig. 10c, fewest on tergite 9; median longitudinal, dark-brown line on tergites 7-9 interrupted by posteromedian elevations (fig. 9a); small reddish-brown tubercles on tergites 7-10; lateral margins of segments 6-9 finely crenulate with few minute hairs. Sterna yellowish with extensive dark-brown mottling, least on sternite 9 (fig. 10d); an inconspicuous dark-brown spot near lateral borders of sternites 2-6 (fig. 10d). Posterolateral projections on segments 6-9 weakly developed, largest on segment 9; posteromedian elevation on tergites 7-9 weakly developed, largest on 9 and extending approximately 1/5 the length of tergite 10. Caudal filaments yellow with pronounced dark-brown basal band (fig. 10c).

**Variations:** Except for the difference in the depth of the apical cleft of female sternite 9 in which one of the three available female imagoes has a distinctly shallower apical cleft than the others, no other variation was noted among the adults.

Nymphal variations include the general body color, marking on the labrum and abdominal tergite 10, and varying degrees of markings on abdominal sternite 9. Nymphs are generally yellowish-brown except a few which are dark reddish-brown and have the base of the lateral spines of the mesonotal shield and the dark-brown banded legs greenish-yellow. Several nymphs have a transversely broad, basal black band on the labrum while others lack such marking. Similarly abdominal tergite 10 in some nymphs has dark-brown markings which are lacking in others. Few nymphs have the basal 1/3 of abdominal sternite 9 mottled with dark brown, while others have the basal 1/2 to almost the entire length of the same sternite mottled.
**Figure 5.** a-f. Mouthparts of mature nymph of *B. rogersi*: a. left mandible; b. hypopharynx; c. labium (dorsal view on left, ventral on right); d. right maxilla; e. labrum; f. apex of maxilla, enlarged; g. Fore claw (after Pescador and Peters, 1974).

**Geographical Distribution:** *Baetisca berner* occurs in the Appalachian regions of Virginia, West Virginia, Pennsylvania, and Tennessee (fig. 15a).

**Discussion.** — Tarter and Kirchner (1978) described *B. berner* from mature nymphs and suggested that it appears to be closely related to *B. carolina*. The species is herein redescribed as additional specimens, including adults, were made available to us. The
imagoes are described for the first time, with descriptions based on reared specimens from the type locality.

_Baetisca berneri_ can be distinguished from the other species of the genus by the following combination of characters. In the imagoes: (1) basal 1/3 of forewing and entire hind wing are faintly washed with yellowish-brown; (2) abdominal sternites 2-6 have prominent black, mediolateral spots; and (3) penes are ovate, apically blunt and greatly enlarged basally (fig. 2j). In the nymph: (1) frontal projection is weakly developed (fig. 10c); (2) genal spines are developed, upcurved and sharp pointed (fig. 10c); (3) lateral margins of mesonotal shield are finely crenulate; (4) dorsal projections of mesonotal shield are weakly developed and are distinctly lower than medial hump (fig. 4b); and (5) abdominal terga have dark-brown spots similar to those shown in fig. 10c, and sternae are extensively mottled with dark brown.

_Baetisca berneri_ appears to be most closely related to _B. carolina_ but can be distinguished from it by the apparently lighter wing color in _berneri_ and the pronounced dark-brown bandings of the nymphal caudal filaments.

Absence of more distinctive morphological characters to differentiate _B. carolina_ and _B. berneri_ casts some doubts as to the definitive species status of the latter. The species could very well be a variant of _carolina_. An in-depth comparative study of the biology and ecology of both species is necessary to develop a more accurate assessment of their relationships.

The uncertain status of _B. callosa_ and the possibility of _B. berneri_ being a synonym of it is pointed out in the discussion of _callosa_. Immature nymphs of both species are similar and representatives of _B. callosa_ are presently known only in this early stage of development.

**Biology** and **Ecology.** — The nymphs seem to prefer slowly to moderately flowing water where they live on a substrate mixture of sand, gravel, and small stones (Tarter and Kirchner 1978). Reared adults emerged in April and May and nymphs were collected from March to October.

*Specimens Examined:* PENNSYLVANIA: Columbia Co: Raven Creek, 6 V 77 (N) (FSCA), West Creek, 29 VI 76 (N) (FSCA). Luzerne Co: Huntington Creek, 27 VII 76 (N) (FSCA), 30 VIII 77 (N) (FSCA). Sullivan Co: Loyal Sock Creek, 16-20
Figure 6. Gills of mature nymph of B. rogersi: a. gill 1; b. gill 2; c. gill 3; d. gill 4; e. gill 5; f. gill 6 (after Pescador and Peters, 1974).
Baetisca callosa Traver  


After making a very careful study of paratypes of *Baetisca callosa* collected from West Virginia by Dr. J.G. Needham, we have now concluded that the species is not recognizable. Needham’s specimens, studied and described by Dr. J.R. Traver, were less than half-grown nymphs which, at the time of Traver’s work, appeared to her to be distinctive; we now know they are not. She distinguished the species in 1931 as a “small nymph, lacking both dorsal and lateral spines on the mesonotal shield, and with prominent black bands across basal portion of setae. Very short frontal processes.”

Our examination of young nymphs of various species has shown frequently that specimens which could be identified as *callosa* were collected along with more mature, easily identifiable older nymphs. For example, specimens of *B. lacustris* from Wisconsin and *B. laurentina* from Manitoba and Alberta included young nymphs which, had they not been taken with the older ones, would have been identified as *callosa*.

*Two paratype nymphs of B. callosa* which Dr. Traver had given to Dr. Richard Daggy when he was a graduate student at the University of Minnesota were made available to us. Daggy recognized the difficulties with *callosa* when he wrote in his discussion of *B. laurentina* (1941, p. 242):

A series of 31 immature naiads collected from the Churchill River, Manitoba, August 5, 1937 (RHD), are tentatively placed here. They
do not have the dorsal and lateral spines developed more than as rounded tubercles. In size, they correspond to two *B. callosa* Traver paratypes kindly given the writer by Dr. Traver.

From examination of immature naiads of *B. laurentina* and other *Baetisca* species, it seems to the writer that *callosa* Traver merely represents a very young stage of some species probably already described — perhaps *carolina* Traver. The particular species and synonymy involved will have to be worked out by careful rearings from the type locality in West Virginia.

As we studied the two paratype nymphs, it became clear to us that one of them might well be a young specimen of the recently named *B. berner* Tarter and Kirchner. The second nymph was not sufficiently mature to call it anything other than *B. callosa*. Because of the uncertainty of just what Traver was describing, we have decided to assign the name *callosa* to no further specimens. Perhaps someone will be able at a later date to follow Dr. Daggy's suggestion of rearing specimens from the type locality and will finally be able to resolve the enigma.


**Baetisca (Baetisca) carolina** Traver

*Figures 2j, 7b, 9b,c,f,g, 11b, 15a*


**Male Imago** (in alcohol). — *Length:* body, 8.0-10.0 mm; forewing, 8.0-11.0 mm; caudal filaments, 6.5-7.8 mm.

*Head:* Brownish-yellow. Antennae yellowish; Eyes almost contiguous dorsally.

*Thorax:* Pronotum yellowish. Mesonotum yellowish, median longitudinal suture darker and translucent; outer and inner parapsidal furrows brown, base and submedian areas of scutellum reddish-brown, almost black underneath. Metanotum brown. Sterna yellowish, darker along margins; mesosternum translucent, colorless.

*Wings:* Longitudinal veins of fore- and hind wings light brown, basal 1/3 darker, stigmatic area of forewing opaque white; basal 1/2 of fore- and hind wings faintly flushed with reddish-brown.

*Legs:* Fore legs pale yellow to greenish-white, claws darker. Meso- and metathoracic legs yellowish, progressively paler toward tarsi; tarsal joints with pale brown band; claws shiny brown.

*Trans. Amer. Ent. Soc., Vol. 107*
Abdomen: Terga brownish-yellow to purplish-brown, darker on tergites 1-6; pleural fold with granulate dark-brown markings. Sterna pale yellow to light brown; sternites 2-6 with prominent black spot near lateral borders, reduced and elongate on sternite 6. Genital forceps yellowish. Penes dark yellow, lanceolate, apically blunt and gradually enlarged basally (fig. 2d). Cerci pale yellow, darker towards base; vestigial median filament pale yellow to reddish-brown.

**Female Imago (in alcohol).** — Length: body, 9.0-11.0 mm; forewing, 10.0-12.0 mm; caudal filaments, 5.0-6.0 mm.

**Head:** Yellowish, faintly flushed with brown. Antennae yellowish.

**Thorax:** Color slightly paler than that of male, markings similar. Color of wings and legs as in male; prosternal process less bifid than in male. Cerci and vestigial median filament yellowish.

**Mature Nymph (in alcohol).** Length: body, 8.5-13.9 mm; caudal filaments, 2.0-3.0 mm.

**Head:** Yellowish to light brown with brown mottling and small, dark-brown tubercles; black spot between base of eye and genal spine. Frontal projection weakly developed, almost truncate apically (fig. 11b). Genal spines well developed and with upcurved brown tips (fig. 11b); clearly visible when viewed dorsally. Antennae yellowish, distal flagellar segments darker.

**Thorax:** Mesonotal shield broad with ratio of length to width 1.2:1.0. Anterolateral and lateromedial lobes weakly developed (fig. 4a); lateral spines approximately 1.5 times as long as width at base, sharp pointed (fig. 11b); dorsal projections weakly developed (fig. 7b) and distinctly lower than medial hump. Mesonotal shield yellowish with small, dark-brown tubercles and brown oblique markings similar to fig. 11b, ventral margins with brown mottling, cluster of small...
pale yellow circular spots near anterolateral corners; lateral margins finely crenulate. Sterna yellowish with brown mottling and dark brown tubercles.

Legs: Coxae brown, claws shiny brown, remainder of segments yellowish; venter of femora with dark-brown tubercles; tibiae with basal brown band; tarsi with median brown band.

Abdomen: Tergites 7-9 brownish-yellow with variable dark-brown markings (figs. 9b,c,f,g); median longitudinal dark-brown line on tergites 7-10 interrupted by posteromedian elevation on tergites 7-9, continuous on tergite 10; prominent black-brown tubercles on tergites 7-10. Lateral margins of segments 6-9 crenulate and with fine hairs. Sterna yellowish with brown markings and small dark-brown tubercles. Posterolateral projections on segments 6-9 weakly developed; posteromedian elevation on tergites 7-9 weakly developed, largest on tergite 9 and extending almost 1/5 length of tergite 10. Caudal filaments yellowish to light brown.

Variations: The nymphs exhibit a few morphological variations. Mature nymphs collected from Tennessee and Virginia and a few from North Carolina generally have a broader mesonal shield and shorter lateral spines than those from South Carolina, Georgia and most of North Carolina. Five nymphs from each of these areas were measured and we found that those from Tennessee, Virginia, and a few from North Carolina have the width of the mesonal shield approximately 9/10 of the maximum length and the lateral spines as long as their width at the base. Nymphs from Georgia, South Carolina, and many from North Carolina have the width of the mesonal shield approximately 4/5 of the maximum length and lateral spines approximately 1.5 to 2 times as long as the width at the base. Nymphs from Georgia were found to have the longest lateral spines (2 times as long as the width at the base) which are slightly slanted posteriorly so that they resemble the wings of a jet airplane.

Variations in thoracic notal shield and abdominal tergal markings are common in B. carolina. Nymphs from South Carolina and a few from North Carolina have broader and more solid oblique brown markings on the mesonal shield than the nymphs from Georgia, Tennessee, Virginia, and most of North Carolina. Similarly, nymphs from South Carolina have less extensive, but nevertheless well-defined, abdominal tergal markings (fig. 9c) compared to the more extensive but ill-defined markings of those from other areas (fig. 9b, f, g). Nymphs from Tennessee have entirely dark reddish-brown thoracic and abdominal sterna compared to the yellowish-brown and variously washed with brown nymphs from other localities.

Geographic Distribution: Baetisca carolina occurs in the Piedmont and mountainous regions of Georgia, North Carolina, South Carolina, Tennessee, and Virginia (fig. 15a).

Discussion. — Traver (1931) described B. carolina from reared specimens collected at Big Alamance Creek in the Piedmont area of North Carolina. A year later she discussed the nymphal and subimaginal differences between carolina and obesa using the dorsal spination of the thoracic notal shield, comparative length of the galea-lacinia and the maxillary palpus, and the wing color. Dr.
Traver also discussed the differences between *B. carolina* and *B. rubescens* in the same paper. In their keys to the known species of *Baetisca* nymphs, McDunnough (1932) and Traver (1935) placed *carolina* and *lacustris* in the same couplet using the genal spines, and wing and leg color as diagnostic characters. Berner (1955) used the genal spines and lateral spines of the mesonotal shield and the posterolateral projections of the abdominal segments as characters to differentiate *B. carolina* from *B. escambiensis*.

As recently collected specimens revealed new taxonomic information, the species is herein redescribed. *Baetisca carolina* can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) basal 1/2 of forewing and basal 2/3 of hind wing faintly flushed with reddish-brown; (2) sternites 2-6 have prominent black spots near lateral margins; and (3) penes are ovate, apically blunt and greatly enlarged basally (fig. 2d). In the nymph: (1) frontal projection is weakly developed (fig. 11b); (2) genal spines are well developed, upcurved and sharp pointed (fig. 11b); (3) mesonotal shield has sharp-pointed lateral spines (fig. 11b); (4) dorsal projections of mesonotal shield are weakly developed and distinctly lower than medial hump (fig. 7b); and (5) abdominal tergites 7-9 are brownish-yellow with variable dark-brown markings similar to those shown in fig. 9b,c,f,g.

*Baetisca carolina* is closely related to *B. bernerii* but can be distinguished from it by the darker wing color in the adult stage and the lack of pronounced basal bands on the caudal filaments of the nymph.

**Biology and Ecology.** — Traver (1931) discussed the ecology of *B. carolina* in detail. Nymphs are found mostly in a mixture of loose gravel and sand in beds near the quiet edge of streams. Collection records indicate that the nymphs occur from September through August and adults emerge from April through June.

*Figure 8.* SEM photographs: *a.* and *c.* ventral surface of nymphal femur to show setae, *B. rogersi* — magnification: *a.* x365, *c.* x2165; *b* and *d.* ventral surface of nymphal femur to show setae, *B. escambiensis* — magnification: *b.* x185, *d.* x700; *e.* abdominal tergal surface, *B. escambiensis*, x320; *f.* nymphal caudal filament, *B. rogersi*. 
Figure 9. Variations in nymphal abdominal markings: a. B. berner; b, c, f, g. B. carolina; d, e. B. rogersi; h, i. B. gibbera.
Baetisca columbiana Edmunds


The following description is quoted directly from Edmunds, 1960:102-104:

"Length, body 6 mm., terminal filaments 2 mm. Color. body light brown, with dark brown mottling and spots as in figure 1. Dark spots on venter larger and more sparse than on dorsum. Eyes black. Antennae pale smoky brown. Tails smoky brown. Genal and frontal projections pale, margined with smoky brown. A distinct larger dark spot at the base of the coxal insertion of each meso- and metathoracic leg. The tibiae and tarsi without dark spots. Claws smoky brown, becoming darker apically. Head, with genal projections extending only to front, rounded; frontal projections small, rounded; apex of second segment of maxillary palpi produced into a finger-like projection. Thorax, mesonotum moderately wide and only moderately humped; without lateral mesonotal spines, only a gently rounded protuberance; no dorsal mesonotal spines. Claws moderately long and tapered. Abdomen, tergites 7 and 8 without a median spine, a poorly developed one on 9. Entire body covered with fine tubercles, giving a granular texture; these tubercles are much fainter on the tibiae and tarsi."

Geographical Distribution: Baetisca columbiana is the only species in the genus said to occur west of the Rocky Mountains. Barton (1980) reported collecting columbiana nymphs in lotic habitats near Fort McMurray, Alberta (57° 02’ N, 111° 30’ W); however, the specimens, which were made available to us for study, were found to be B. laurentina, not columbiana.

Discussion. — Edmunds (1960) described B. columbiana based on one nymph collected from the Columbia River, Washington. No other specimen has since been taken and attempts to locate the holotype have been unsuccessful. One of us (MLP) visited the California Academy of Sciences where the holotype was reported to have been deposited but the specimen could not be found. As we have no specimens of columbiana available to us, we have repeated Edmunds’ description for the sake of completeness.

We are dubious as to the correctness of the locality data inasmuch as no other Baetisca nymph has been reported from any site west of the Continental Divide with certainty. We suspect that

Figure 10. Dorsal and ventral views of mature nymphs: a and b. B.becki; c and d. B. berneri.
the collector, J.J. Davis, may have inadvertently confused his locality labels prior to giving the single specimen to Dr. Edmunds. As the matter cannot be resolved at this time, we are presenting all available information about *B. columbiana*.

The locality from which the specimen was reported is given by Edmunds as “Columbia River, Pasco, Franklin County, Washington, November 4, 1948 (J.J. Davis), deposited in collection of California Academy of Sciences, San Francisco.”

**Baetisca (Baetisca) gibbera** Berner

Figures 2h, 7a, 9b,i, 11c, 15c

*Baetisca* sp. Berner 1953:145.


**Male Imago** (in alcohol). — *Length:* body 11.5-11.7 mm; forewing 11.5 mm; caudal filaments 8.5-10.8 mm.

**Head:** Brown. Antennae brown. Eyes yellowish-brown, almost contiguous dorsally.

**Thorax:** Nota brown with scutellum dark brown. Posterolateral lobes of scutum shiny brown, scutellum with a pair of prominent dark-brown spots. Sternum brown.

**Wings:** Longitudinal veins of forewings brown; crossveins colorless, except for those in stigmal and anal areas of forewing which are brownish; membrane of forewing hyaline, base proximal to humeral base brownish; membrane of hind wing hyaline, longitudinal veins brown, membrane brownish at costal angle.

**Legs:** Fore leg grayish-brown, all joints marked with dark brown, fifth tarsal segment and claws dark brown. Meso- and metathoracic legs slightly paler than fore leg; articulations between tarsal segments strongly marked dorsally with brown; fifth tarsal segments darker than others.

**Abdomen:** Terga generally light brown, tergites 2-5 and including anterior 1/4 and posterior margin of tergites 6-8 dark brown, remainder paler. Sternal brown with posterior margins dark brown, darkest on sternites 6-8, giving annulate appearance to abdomen; sternites with broad, brownish, elongate, anterolateral markings, most prominent on anterior segments and gradually decreasing in size posteriorly. Genital forceps and penes grayish-brown; penes deltoid, apically pointed, base gradually enlarged proximally (fig. 2h). Caudal filaments tinted with brown, basal 1/4 darker, articulations brown.

**Female Imago** (in alcohol). — *Length:* body 11.6 mm; forewing 16.1 mm; caudal filaments 8.0 mm. Color pattern of female similar to that of male.

**Mature Nymph** (in alcohol). — *Length:* body 6.3-12.0 mm; caudal filaments 1.8-3.5 mm.
Head: Brown; covered with small tubercles. Frontal projection not strongly produced, rounded. Genae broadly produced and flared (fig. 11c). Antennae pale, washed with brown, tip darker.

Thorax: Mesonotal shield broad, ratio of length to width 1.0:1.2; lateral margins of mesonotal shield anterior to lateral spines sinuously curved with no distinct lobes (fig. 11c); lateral spines short (length as long as width at base), blunt or slightly pointed; dorsal projections and medial hump absent (fig. 7a); mesonotal shield light brown with irregular brown mottling and median pale spots; margins finely crenulate. Sterna light brown with large dark-brown patches anterior and posterior to mesothoracic legs, smaller patches medial to metathoracic legs.

Legs: Coxae and trochanters brownish, femora dark brown basally becoming lighter distally; basal 1/2 of tibiae banded with brown; tarsi with median, brown band; claws deep amber.

Abdomen: Terga brownish; tergites 7-9 with dark-brown mottling or spots similar to those shown in figs. 9_h,i; broad, longitudinal, median, dark-brown line on tergites 7-9 interrupted by small posteromedian elevation. Sterna brownish, tuberculate. Posterolateral projections on tergites 7-9 weakly developed. Caudal filaments light brown.

Variations: Nymphs of B. gibbera exhibit a number of morphological variations which occur throughout the range of the species or which may be geographically confined. Nymphs collected from Virginia [10.5 mm. (9.0-12.0 mm.) mean body length] are larger than those from Florida, Georgia, and Mississippi [6.9 mm. (6.3-7.5 mm.) body length]. Additionally nymphs from Virginia have brownish antennae, tergal markings similar to those shown in fig. 9_i, and abdominal sterna mottled with brown, while the Florida, Georgia, and Mississippi have pale antennae faintly washed with brown, abdominal tergal markings similar to those shown in fig. 9_h, and unmottled abdominal sterna.

More specifically, nymphs of B. gibbera from Florida, Georgia, and Mississippi show the following variations from the average given in the above description. Lateral mesonotal spines may be very short and very blunt to somewhat more elongate but still blunt. Mesonotum may be tan spotted with brown; thoracic sternum spotted. Legs may have coloration reduced to strong brownish mark at outer edge of tibiae; coxae and trochanters brown and femora brown except at extreme distal ends; tibiae dark-banded basally and tarsi with pale brown band at middle. In some specimens legs may be pale, except for a dark spot at outer margin of tibiae and an indication of a brown band at middle of tarsus. Abdominal sternites 1-7 brownish and stippled with darker brown, 8 and 9 paler.

Variations among the nymphs from Virginia include markings and lateral spines of the mesonotal shield, and color of legs, abdomen, and caudal filaments. Mesonotal shield of nymphs varies from being almost solid brown with a pair of median pale spots to randomly mottled with brown. The lateral spines of the mesonotal shield are mostly blunt but a few nymphs have them with somewhat more pointed tips. Some nymphs have dark-brown legs with the distal portion of the tibiae paler than the femora; others have the coxae, trochanters, and femora heavily mottled with brown. Several specimens have tergites 7-9 (fig. 9_h,i) and sterna mottled with brown, others have almost solid brown tergites and sternites. Furthermore, caudal
filaments of some nymphs are dark brown but gradually become paler distally; in others the filaments are uniformly brownish.

**Geographical Distribution:** Available records indicate that *B. gibbera* has a disjunct distribution. The species occurs in Florida, Georgia, Mississippi, Tennessee, and Virginia (fig. 15c).

**Discussion.** — No further taxonomic account of *B. gibbera* has been published since its original description (Berner, 1955). Collection of more specimens from several localities, including reared adults, produced additional taxonomic data which facilitate a redefinition of the species. The imagoes, described for the first time, were reared from nymphs taken from Tom's Creek, Montgomery County, Virginia.

*Baeotisca gibbera* can be distinguished from the other species of the genus by the following combination of characters. In the imagoes: (1) membranes of fore- and hind wings are hyaline; (2) posterior margins of abdominal sternites are dark brown, darkest on sternites 6-8 giving an annulate appearance to the segments; and (3) penes are deltoid, apically pointed and enlarged basally (fig. 2h). In the nymphs: (1) frontal projection is developed and prominent (fig. 11c); (2) genae are broadly produced and flared (fig. 11c); (3) mesonotal shield has short lateral spines having the length subequal to width (fig. 11c); (4) mesonotal shield lacks dorsal projections and medial hump (fig. 7a); and (5) thoracic and abdominal sterna have variable markings as indicated in the description and under the section on variations.

*Baeotisca gibbera* is a sister species of *B. rogersi* and *B. becki* but can be distinguished from them by any of the following characters. In the imagoes; (1) the fore- and hind wings are hyaline; and (2) the penes are deltoid, apically pointed and enlarged basally (fig. 2h). In the nymph: (1) length of mesonotal shield is subequal to width and the lateral spines are short (fig. 11c); (2) mesonotal shield lacks dorsal projections and medial hump (fig. 4a,b) and (3) abdominal sterna have no defined markings.

**Biology and Ecology.** — Nymphs of *B. gibbera* have been collected from the cool mountain streams of the Appalachian Moun-

**Figure 11.** Dorsal views of mature nymphs: *a.* *B. rogersi; b.* *B. carolina; c.* *B. gibbera* (after Berner, 1955).

**TRANS. AMER. ENT. SOC., VOL. 107**
tains as well as the warm waters of the Coastal Plain. Nymphs are found in rather swiftly flowing streams where they live beneath logs and among pebbles in riffles (Berner, 1955; Berner and Pescador, 1980). The nymphs have been collected from September through April and adults have been reared in March and April in Virginia.


**Baetisca (Baetisca) lacustris** McDunnough

Figures 2h, 3e, 13a,b, 15b


*Baetisca obesa* (Say); Clemens 1913:331; 1915:119.


**Male IMAGO** (in alcohol). — **Length**: body 6.5-9.0 mm; forewing 9.0-10.5 mm; caudal filaments 5.0-8.0 mm.

**Head**: Brown. Antennae brown. Eyes contiguous dorsally.

**Thorax**: Nota pale grayish to brown; scutellum brown with margins darker. Sterna pale to light brown.

**Wings**: Longitudinal veins of fore- and hind wings usually colorless, sometimes with light brownish tint in C, Sc, and R, of forewing; membrane hyaline.

**Legs**: Tan, washed with grayish-brown in some specimens; fore tarsi narrowly annulate with brown at each joint, meso- and metatarsi with trace of narrow, dark ring at each joint; claws pale to brownish.

**Abdomen**: Terga white to grayish-brown, chalky-white laterally on tergites 7-10 in most individuals. Sterna pale. Genital forceps pale to brownish. Penes deltoid, apically pointed, base gradually enlarged (fig. 2h). Caudal filaments white to light brown.

**Female IMAGO** (in alcohol). — **Length**: body 6.5-8.5 mm; forewing 9.0-10.5 mm; caudal filaments 5.0 mm.

Female very similar to male in color pattern, differing only in sexually dimorphic traits.

**Mature NYMPH** (in alcohol). — **Length**: body 6.8-10.2 mm; caudal filaments 2.1-3.0 mm.

**TRANS. AMER. ENT. SOC., VOL. 107**
Head: Tan with pronounced brown freckling; small occipital tubercles. Frontal projection small, anterior and posterior areas slightly depressed. Genal shelf prominent and rounded at outer angle (fig. 13b). Antennae pale.

Thorax: Mesonotal shield relatively broad, ratio of length to width 1.4:1.0; lateral spines long, approximately 1.8 times as long as width at base, sharp pointed (fig. 13a); dorsal projections weakly developed, distinctly lower than medial hump (fig. 4b); mesonotal shield tan, overlaid with extensive brown mottling. Sterna tan with large brown spots; conspicuous brown spots between pro- and mesocoxae and meso- and metacoxae (fig. 13b).

Legs: Light tan with few brown spots on femora; tibiae with basal brown markings, almost completely encircle the metatarsus.

Abdomen: Tergites 7-9 and posterior 1/2 of tergite 6 with scattered brown spots; brown, median, longitudinal line on anterior 1/2 of tergites 7-9, barely evident on tergite 10. Sterna tan with scattered brown spots, becoming less numerous posteriorly (fig. 13b). Posteriolateral projections and posteromedian elevations on tergites 7-9 weakly developed. Caudal filaments pale.

Variations: Some nymphs have freckling greatly reduced and in rare individuals the brown spots between the coxae may be absent while in others the spots are large and elongate. The median brown line on tergites 7-9 is sometimes obsolescent or may extend the full length of the tergite. Occasionally the lateral mesonotal spines may be rounded at the tip rather than sharp pointed; in some individuals the spines are rather long and pointed and in others they are relatively short. At times the anterior edge of the lateral mesonotal spines is curved and the posterior edge straight, but usually both edges are straight. The dorsal ridges of the mesonotum of some individuals may be rather prominent and show a rather strong degree of tuberculation; in others the tuberculation may be scarcely noticeable. The legs may lack brown markings at the base of the tibia or the markings may be reduced to no more than a spot.

Geographical Distribution: Baetisca lacustris is widely distributed in middle North America having been collected from the Great Lakes region and across the United States and Canada to the eastern slope of the Rocky Mountains (fig. 15b).

Discussion. — After a careful study of nympha! exuviae identified by Dr. McDunnough (1932) as those of his new species lacustris, we are convinced that B. bajkovi Neave is synonymous with it. Burks (1953) almost synonymized the two when he wrote “This species differs from lacustris only by minor and possibly integrating characters both in the nymph and the adult. It may, thus, eventually be necessary to place bajkovi as a synonym of lacustris”. We now take this action.

Figure 13. Dorsal and ventral views of mature nymphs: a and b. B. lacustris; c and d. B. laurentina.
Traver (1935, in Needham, Traver, and Hsu) devoted only three lines to a description of the nymph of lacustris and Burks (1953) did little better. Neave (1934) distinguished bajkovi from lacustris on the basis of the frontal projections and the genal shelf, which he presumed was better developed in bajkovi. We do not believe these characters are sufficiently distinctive to separate the nymphs into two species.

Daggy (1945) found a useful character to identify the nymphs (earlier pointed out by Neave in his description of bajkovi) in the presence of a large “black dot between the second and third pairs of coxae . . .” (fig. 13b). We have seen the trait on McDunnough’s nymphal exuviae of lacustris as well. On the basis of adult specimens reared from bajkovi nymphs, Daggy described the adult stage and deduced that the imagoes of bajkovi are larger than those of lacustris and that the “apical abdominal terga are not ruddy-tinged as described for that species.” Size is much too variable a character to be used for differentiating species as similar as these and certainly the ruddy-tinged abdominal terga fall in the same category.

Habitat distinctions, likewise, are not necessarily valid for separating lacustris from bajkovi. We believe that the vagility of the nymphs would allow them to inhabit wave-beaten lake shores as well as streams.

Baetisca lacustris can be distinguished from the other species of the genus by the following combination of characters. In the imagoes: (1) membrane of fore- and hind wings are hyaline; (2) abdominal terga are white to grayish-brown and have no pronounced markings; and (3) penes are deltoid, apically pointed and gradually enlarged basally (fig. 2h). In the nymph: (1) frontal projections are small and areas anterior and posterior to the projections are slightly depressed (fig. 13b); (2) genal shelf is prominent and rounded at outer angle (fig. 13b); (3) dorsal projections of mesonotal shield are weakly developed and distinctly lower than medial hump (fig. 4b); and (4) thoracic and abdominal sterna have large brown spots (fig. 13b).

Baetisca lacustris appears most closely related to B. laurentina and B. obesa. Except for the apically pointed, deltoid penes of B. lacustris and B. laurentina, compared to the apically blunt,
lanceolate penes of _B. obesa_, the imagoes of these are almost indistinguishable. The subimaginal wings of _B. lacustris_ appear to have somewhat more extensive white markings than do those of _B. laurentina_ and _B. obesa_.

The nympha of _B. lacustris_ can be separated from those of _B. laurentina_ and _B. obesa_ by any of the following characteristics: (1) frontal projections are small and weakly developed (fig. 13a); (2) mesonotal shield is relatively broad (fig. 13a) and has weakly developed dorsal projections (fig. 4b); and (3) entire body is covered with brown spots (fig. 13a, b).

_Biology and Ecology._ — Collection records indicate that the adults of _B. lacustris_ emerge from May through July. Nymphs have been found from October to July.


**Baetisca (Baetisca) laurentina** McDunnough

Figures 2h, 13c,d, 15b


**Male Imago** (in alcohol). — **Length:** body 8.8-10.8 mm; forewing 10.7-12.8 mm; caudal filaments 8.0-10.0 mm.

**Head:** Brown. Antennae light brown. Eyes almost contiguous dorsally.

**Thorax:** Mesonotum dark brown, scutellum ranging from dark brown to almost black. Sterna light brown.

**Wings:** Longitudinal veins of fore- and hind wings brown, crossveins colorless; membrane hyaline with brownish tint at extreme base; stigmatic area of forewing opaque and bullae prominent.

**Figure 14.** a and b. Dorsal and ventral views of *B. rubescens*; c. diagram to show phylogenetic relationships in the genus *Baetisca.*
### TABLE 1. Character State of Figure 14 (D = derived; P = primitive)

<table>
<thead>
<tr>
<th>Furcation 1</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eyes</td>
<td>A</td>
</tr>
<tr>
<td>Penes</td>
<td>(P) uniformly colored</td>
</tr>
<tr>
<td>Mesonotal shield</td>
<td>(P) gradually tapered</td>
</tr>
<tr>
<td>Frontal projection</td>
<td>(P) not dorsoventrally compressed</td>
</tr>
<tr>
<td></td>
<td>(D) present</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Furcation 2</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genae</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>(D) broadly produced, strongly flared to sharp-pointed</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Furcation 3</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genae</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>(P) broadly produced and strongly flared</td>
</tr>
<tr>
<td>Frontal projection</td>
<td>(D) developed</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Furcation 4</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wings</td>
<td>A</td>
</tr>
<tr>
<td>Mesonotal shield</td>
<td>(P) hyaline</td>
</tr>
<tr>
<td>Lateral spines</td>
<td>(D) length subequal to width</td>
</tr>
<tr>
<td>Dorsal projection</td>
<td>(D) short (length subequal to width)</td>
</tr>
<tr>
<td></td>
<td>(D) absent</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Furcation 5</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Penes</td>
<td>A</td>
</tr>
<tr>
<td>Lateral spines</td>
<td>(D) ovate</td>
</tr>
<tr>
<td></td>
<td>(P) sharp-pointed</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Furcation 6</th>
<th>Lineages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesonotal shield</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>(P) broad (length less than 1-1/2 X width)</td>
</tr>
<tr>
<td>Dorsal projection</td>
<td>(D) weakly developed</td>
</tr>
<tr>
<td>Lateral spines</td>
<td>(P) long</td>
</tr>
</tbody>
</table>

---

**Legs:** Yellowish to light brown; brown at articulations of meso- and metathoracic legs.

**Abdomen:** Terga light brown to brown; sterna paler, whitish on sternites 7-9 in some specimens. Genital forceps brown. Penes deltoid, apically pointed, base gradually enlarged (fig. 2h). Caudal filaments brownish, darker at articulations.
FEMALE IMAGO (in alcohol). — *Length:* body 8.3-12.3 mm; forewing 8.8-15.6 mm; caudal filaments 5.0-8.3 mm.

*Head:* Grayish-brown, rarely whitish. Antennae light brown.

*Thorax:* Color and markings as in male imago, except generally paler.

*Wings:* Color and markings as in male imago.

*Legs:* Yellowish, except tarsi tinted with grayish-brown; tarsal articulations brown, claws brown.

*Abdomen:* Terga light brown, sterna paler. Caudal filaments narrowly annulate with light brown.

MATURE NYMPH (in alcohol). — *Length:* body 8.3-9.7 mm; caudal filaments 2.2-2.8 mm.

*Head:* Dorsum mottled with brown, posterior margin dark brown. Frontal projection developed, bifid with each part depressed dorsally and divergent, extended forward to at least the level of anterior margin of head; prominent ridge anterior to frontal projection. Genae slightly produced outwards and angulate. Antennae yellowish, distal segments brown.

*Thorax:* Mesonotal shield relatively long and narrow, ratio of length to width 1.6:1.0. Anterolateral and lateromedial lobes weakly developed (fig. 4a); lateral spines relatively short, about as long as width at base, rounded at tip; dorsal projections prominent and divergent (fig. 4b), higher than medial hump; anteromedial hump absent (fig. 4b). Mesonotal shield mottled with brown (fig. 13c), ventral margin strongly outlined with dark brown (fig. 13d). Sterna mottled with brown (fig. 13d).

*Legs:* Brown. Femora slightly darker than other leg segments.

*Abdomen:* Tergites 7-9 extensively mottled with brown laterally; tergal pigmentation most intense on posterior portion of 6, least on tergite 10 with base of segment dark brown; median brown line on tergites 7-9. Sterna with scattered brown mottling (fig. 13d). Posterolateral projections of segments 6-9 weakly developed, largest on 9 but not extended beyond posterior extension of subanal plate; posteromedian elevations on tergites 7-9 weakly developed. Caudal filaments brown.

*Variations:* Forewing of female imagoes from Louisiana have the basal 2/3 of the anal area and the basal portion of the cubito-anal space clouded with brown in the forewing, as well as having the crossveins in these areas brown; the hind wing is also light brown at the base. Specimens from other areas have the membrane hyaline and the crossveins are colorless.

Younger nymphs have smaller frontal projections and a less prominent genal shelf than the mature ones. Mature female nymphs have a pair of occipital tubercles that may be very low and inconspicuous or, in some, rather conspicuous. Additionally, the lateral spines of the mesonotal shield may be either relatively long and sharp or short and rounded; dorsal spines may be reduced to strong elevations but with a tendency toward a spinose condition. Nymphal color varies from dark brown to pale overlaid with varying degrees of mottling. These variations exist throughout the distributional range of the species.

*Geographical Distribution:* *Baetisca laurentina* is widely distributed occurring in many areas of eastern North America, the Great Plains, and through Canada into the Northwest Territories (fig. 15b).
Discussion. — Although *B. laurentina* has been known since 1932, no really adequate description of the stages has been given. McDunnough’s few lines devoted to the species are insufficient to permit recognition of the species. Traver (1935) used less than 3 lines to describe the nymph. While Daggy’s doctoral dissertation (unpublished) helped some, there is still confusion in identifying the various stages. We are, therefore, presenting a fuller description of the external morphology of the imago and nymph. Further, we have used the same nymphs we presume McDunnough had
before him when he described the species and are adding variations that we have observed to occur in specimens from various parts of North America.

*Baetisca laurentina* can be distinguished from the other species of the genus by the following combination of characters. In the imagoes: (1) fore- and hind wings are hyaline except for those of the female imagoes from Louisiana which are clouded with brown at the base; (2) abdominal terga lack distinct markings; and (3) penes are deltoid, apically pointed, and gradually enlarged basally (fig. 2h). In the nymph: (1) frontal projection is prominent and bifid with each part depressed dorsally and divergent; projection extends forward to at least the level of the anterior margin of head (fig. 13c); (2) genal shelf is strongly flared and angulate (fig. 13d); (3) mesonotal shield has relatively short spines which are as long as width at the base, rounded at tip; (4) spinous dorsal projections are distinctly higher than medial hump (fig. 4b); (5) thoracic and abdominal sterna are mottled with dark brown; and (6) mesonotal shield has strongly outlined solid dark-brown ventral margin (fig. 13d).

*Baetisca laurentina* appears to be closely related to *B. obesa* but can be distinguished from it by any of the following characters. In the imagoes: (1) abdominal terga lack brown mottling and (2) penes are deltoid and apically pointed (fig. 2h). In the nymph: (1) genal shelf extends forward to at least the level of anterior margin of head (fig. 13c); (2) frontal projection is similar to that shown in fig. 13c; and (3) the ventral margin of the mesonotal shield is strongly outlined with dark brown (fig. 13d).

**Biology and Ecology.** — Berner and Pescador (1980) briefly summarized published accounts describing the nymphal habitats of *B. laurentina*. Collection records indicate that in Canada the adults emerge from April through June and in the United States from March to August. Nymphs have been collected from September through August throughout the distributional range.


TRANS. AMER. ENT. SOC., VOL. 107
Baetis obesa (Say)
Figures 2i, 7c, 12a, 15b

Baetis obesa Say 1839:378; Picket 1843:195; Walker 1853:563; LeConte 1859:412; Hagen 1861:45.

Baetis obesa; Walsh 1862:378; 1863:187; 1864:200; Eaton 1868:69; 1871:101; 1885:228; Packard 1870:595; Joly 1880:157; Vayssiére 1881:4; 1882:99;

**Male Imago** (in alcohol). — **Length:** body 6.0-8.0 mm; forewing 8.0-10.0 mm; caudal filaments 6.0-7.5 mm.

**Head:** Dark brown. Antennae brown. Eyes contiguous dorsally.


**Wings:** Longitudinal veins of fore- and hind wings colorless except C, Sc, and R, of forewing brownish basally. Membrane hyaline; stigmatic area opaque.

**Legs:** Tan; tarsal segments narrowly annulate with brown, claws brownish; femora lightly washed with brown.

**Abdomen:** Terga heavily mottled with brown, strongest concentration on tergites 1 and 2. Sterna paler than terga, mottled with brown laterally; sternites 7-9 rather pale medially. Forceps pale. Penes yellowish, lanceolate, apically blunt and gradually enlarged basally (fig. 2i). Caudal filaments pale with brown annulations at articulations; vestigial median filament dark brown.

**Female Imago** (in alcohol). — **Length:** body 7.0-9.0 mm; forewing 9.0-12.0 mm; caudal filaments 5.5-7.0 mm.

**Head:** Pale brown, mottled with purplish-brown. Antennae purplish-brown.

**Thorax:** Mesonotum brown with wide darker brown median stripe; scutellum dark brown. Sterna light brown.

**Wings:** Color of veins and membrane as in male.

**Legs:** Light brown washed with darker brown, most noticeable on femora; markings of tarsal segments as in male.

**Abdomen:** Terga purplish-brown, darkest on tergites 2-6; tergites 7-10 with submedial and posterolateral white areas. Sterna pale with dark-brown, lateral lines running length of segment; similar horizontal lines on intersegmental membranes except at middle. Caudal filaments as in male.

**Mature Nymph** (in alcohol). — **Length:** body 7.6-10.2 mm; caudal filaments 2.3-2.6 mm.

**Head:** Covered with brown mottling. Frontal projection bifid, long, extended well beyond anterior margin of head (fig. 12a), excavated dorsally. Genal shelf small, rounded at anterolateral edge. Male nymphs with vestiges of a pair of oc- cipital tubercles between compound eyes; more prominent in female nymphs. Antennae yellowish.

**Thorax:** Mesonotal shield relatively long and narrow, ratio of length to width approximately 1.7:1.0; lateral spines relatively short, may be straight or slightly recurved posteriorly (fig. 12a); dorsal spines well developed and distinctly higher than medial hump (fig. 7e). Mesonotal shield tan, mottled with dark brown continuing to ventral edge. Sterna pale medially, heavily mottled with dark brown laterally.
Legs: Femora heavily mottled with brown, pale at extreme distal margin; tibiae pale with median, brown band; tarsi with brown median band; claws pale, tip orange brown.

Abdomen: Tergites 6-9 with broad lateral longitudinal dark-brown band, middle pale; anteromedian brown dash on tergites 7 and 8. Sterna heavily mottled with brown, less concentrated medially; sternite 9 with brown coloration concentrated laterally; sternites 2-6 with prominent dark-brown spot near lateral margins. Posterolateral projection on segments 7-9 moderately developed; posteromedian elevation on tergites 7-9 weakly developed. Basal 1/3 of caudal filaments brownish, remainder pale.

Variations: Slight color differences were observed among the imagoes of *B. obesa*. In some individuals pigmentation in veins C, Sc, and R, of the forewing may extend as far as the stigma and in the area basal to the humeral brace they may be dark brown. Occasionally there may be light pigmentation in all the main veins. The hind wings of some specimens are dark brown at the extreme base but in others they may be entirely hyaline. Most female imagoes have broad, lateral, longitudinal, dark-brown markings on the abdominal sternites, including transverse dark-brown lines on the intersegmental membranes; others have these markings obscured.

No notable variations were observed among the nymphs except that a few specimens have relatively short lateral and dorsal spines on the mesonotal shield; these are also sometimes blunt. Occipital tubercles are occasionally obsolete.

Geographical Distribution: *Baetisca obesa* has the widest geographical range of all the species of the genus. It occurs as far south as Florida and Louisiana and northward to Massachusetts, through the central United States into Wisconsin and Minnesota (fig. 15b).

Discussion. — *Baetisca obesa* can be distinguished from the other species of the genus by the following combination of characters. In the imagoes: (1) membrane of fore- and hind wings are hyaline; (2) abdominal terga mottled with brown or purplish-brown; and (3) penes are lanceolate, apically blunt, and gradually enlarged basally (fig. 2i). In the nymph: (1) frontal projections are long, extending well beyond the anterior margin of the head (fig. 12a); (2) the genal shelf is small and broadly rounded at the anterolateral edge; (3) the dorsal projections of the mesonotal are well developed, spinous, and distinctly higher than the medial hump (fig. 7c); and (4) abdominal tergites 6-9 have broad, lateral, longitudinal, dark-brown bands and sternites 2-6 have prominent dark-brown spots near their lateral margins.

*Baetisca obesa* appears to be most closely related to *B. laurentina* but can be distinguished from it by any of the following combination of characters. In the imagoes: (1) abdominal terga have prominent brown mottling; and (2) the penes are lanceolate and apically
blunt (fig. 2i). In the nymph: (1) frontal projections are strongly developed, long, and clearly extended well beyond the anterior margin of the head (fig. 12a); (2) the genal shelf is small and broadly rounded at the anterior lateral edge; (3) the ventral margin of the mesonotonal shield is not outlined with solid markings; and (4) sternites 2-6 have prominent dark-brown spots near the lateral margins.

**Biology and Ecology:** Nymphs of *B. obesa* live in a wide variety of habitats. They occur on the underside of submerged rocks, logs, and among packed leaves in rapidly running streams, as well as in moss attached to submerged tree trunks and in residual, stagnant pools in flooded areas of river flood plains. Our collection records indicate that the nymphs may be found from October through June and adults emerge from January in the south until June in the north. Records of adult emergence in January and February were from laboratory reared specimens.

MAYFLY FAMILY BAETISCIDAE


*Baetisca* (Baetisca) *rogersi* Berner

Figures 1, 2i, 3a,b,c,d,f, 4b, 5, 6, 7d, 8a,c,f, 9d,e, 11a, 15c


**MALE IMAGO** (in alcohol). — *Length*: body 6.5-9.0 mm; forewing 8.0-9.5 mm; caudal filaments 5.5-7.0 mm.

**Head**: Dark brown, posterior margin of vertex darker, genae pale yellow near base of eyes. Scape and pedicel of antennae brown, flagellum pale yellow. Eyes almost contiguous dorsally.

**Thorax**: Pronotum brown with yellow, longitudinal, median line; mesonotum brown with minute black stippling, median area, parapsidal furrows, margins and posterolateral corners dark reddish-brown. Metanotum brown. Sterna grayish-yellow, prosternum brown; minute black stippling between meso- and metasterna; prosternal process reddish-brown.

**Wings**: Longitudinal veins of fore- and hind wings amber, pale near margins; basal 1/3 of forewings and basal 3/4 of hind wings reddish-brown, base almost blackish-red; stigmatic area of forewings opaque white.

**Legs**: Greenish-yellow to yellowish-brown, dorsum of meso- and metathoracic legs washed with brown, tarsal joints with dark-brown transverse band.

**Abdomen**: Terga light reddish-brown; tergites 1-6 darker, particularly remnants of gill attachments and pleural folds; tergites 7-9 with prominent anterior marginal black band extending across tergite; prominent longitudinal reddish-brown median line on tergites 6-10 continuous to median filament. Sternites 2-8 with fine black stippling near anterior and posterior margins, lateral margins grayish-brown; sternite 9 white. Genital forceps pale. Penes yellowish-white, lanceolate, apically blunt with base gradually enlarged (fig. 2i). Caudal filaments yellowish-brown, basal 2/3 with light brown annulations; vestigial median filament reddish-brown to pale yellow.

**FEMALE IMAGO** (in alcohol). — *Length*: body 7.5-10.0 mm; forewing 9.0-11.0 mm; caudal filaments 5.0-6.0 mm.

**Head**: Color of head and antennae as in male imago.

**Thorax**: Color markings as in male except that inner parapsidal furrows and median longitudinal suture darker; prosternal process paler and shorter than in male.

**Wings**: Color as in male.

**Legs**: Color as in male except base of claws light brown.

**Abdomen**: Color and markings as in male; sternite 9 deeply cleft, depth approximately 1/7 maximum width of sternite. Color of caudal filaments as in male.

**MATURE NYMPH** (in alcohol). — *Length*: body 7.0-10.5 mm; caudal filaments 2.0-2.3 mm.
Head: Brownish-yellow, genal margins and frontal projections paler; prominent black spot between eyes and lateral margins of head. Frontal projection prominent, strongly bifid and extended forward almost to the level of anterior margin of head (fig. 11a); genae strongly flared, broad and rounded (fig. 11a). Antennae yellowish, brownish-yellow at articulations.

Thorax: Mesonotal shield broad, ratio of length to width 1.2:1.0; anterolateral lobe weakly developed; lateromedial lobe well developed (fig. 4a); lateral spines approximately 1.3 times as long as width at base, sharp pointed and with margins serrate (fig. 11a); dorsal projections prominent, height less than to subequal to that of medial hump (fig. 7d). Mesonotal shield yellowish with brown shading; lateral margins crenulate, serrate near base of spines. Sterna yellowish.

Legs: Yellowish, claws shiny brown; tibiae with dark-brown proximal area; broad, light-brown, median band on tarsus.

Abdomen: Tergites 7-9 brownish-yellow with broad, transverse black line extending inward from lateral borders almost to median line (fig. 9d); or broad dark-brown basal spot (fig. 9e); lateral and posterior 1/3 of tergite 6 blackish-brown; narrow, median, longitudinal, black line on tergites 7-10, interrupted by posteromedian elevation on tergites 7-9, continuous to median filament on tergite 10; lateral margins of tergites 6-9 crenulate, weakest on 6. Sterna brownish-yellow, faintly washed with brown near lateral margins, prominent pair of brownish-black spots midway between median and lateral margins of sternites 7-9. Posterolateral projections on tergites 6-9 well developed, largest on 9; posteromedian elevation on tergites 7-9 well developed, almost vertical on tergite 8, curved on tergite 9 and extended almost 1/4 length of tergite 10. Caudal filaments brownish-yellow, slightly darker basally; median filament reddish-brown.

Variations. Nymphs and adults of B. rogersi exhibit morphological variations which occur throughout its distributional range or are geographically confined. Common adult variations include the whitish granulations and femoral color. Several adults, particularly females, have whitish granulations covering certain areas of the body, mostly the thoracic pleura and the abdominal sterna. Female femora may be either greenish-yellow or yellow.

Few variations occur among adults collected from the northern and southern geographical limits of the species. One reared male imago from Little River, Oconee Co., South Carolina has lighter colored wings and vestigial median filament, and less pronounced anterior marginal black bands on tergites 7-9 than those from Alabama and Florida.

Nymphal variations within the geographical range are also common in B. rogersi. Specimens from north Florida, south Alabama, and south Georgia exhibit varying degrees of intensity in their markings on the mesonotal shield and tarsi. Nymphs from the Blackwater River drainage (northwestern Florida and southern Alabama) and from south Georgia have more extensive brown shading on the mesonotal shield than those collected from the southernmost limits of its geographical range — Rocky Comfort Creek and Bear Creek, Gadsden County, Florida. Additionally the nymphs from the Blackwater River drainage and adjacent areas have a well-defined pair of prominent pale yellow basal spots on the medial hump of the mesonotal
shield and an inconspicuous light-brown tarsal band, while these characteristics are absent from the nymphs of Rocky Comfort and Bear Creeks.

Nymphs of *B. rogersi* from South Carolina and north Georgia show variations in the shape of the dorsal projections on the mesonotal shield and in the markings of the abdominal terga. Those collected from Upper Three Runs Creek in South Carolina are similar to those from Alabama and Florida in having a broad, anterior, transverse black line on abdominal tergites 7-9 (fig. 9d) and the dorsal projections of the mesonotal shield are distinctly lower than the medial hump (fig. 9d). Nymphs from the Chattooga River, Oconee County, South Carolina, and Rabun County, Georgia, however, have either a prominent pair of black-brown, anterosubmedian spots (fig. 9e) or longitudinally oblique anterosubmedian, dark-brown stripes on tergites 7-9, and spinous dorsal projections that are subequal in height to the medial hump.

Based on the color of the body tubercles and the median filament and the dorsal markings of the mesonotal shield, *B. rogersi* nymphs can be conveniently grouped into northern and southern forms. The former includes nymphs from north Georgia and South Carolina, while the latter represent those from Alabama, Florida, and south Georgia. The northern form has colorless body tubercles, oblique brown markings on the mesonotal shield (similar to those of *B. carolina* nymphs) and a unicolorous reddish-brown median filament. The southern form has reddish-brown tubercles (most prominent on the posterior 2/3 of the mesonotal shield), scattered brown shading on the mesonotal shield (fig. 11a) and a bicolorous median filament with the basal 1/2 to 2/3 reddish-brown and the remainder brownish-yellow. A more extensive study of the species in Georgia is needed to determine the zone of overlap of these two forms.

Geographical Distribution: *Baetisca rogersi* is a common Coastal Plain species but also occurs in the Piedmont provinces of Georgia and South Carolina with rare incursions into the mountainous area of the latter state (fig. 15c).

Discussion: *Baetisca rogersi* was described from reared specimens collected from a sand-bottom creek in northwestern Florida (Berner, 1940). The biology and ecology of the species were reported in detail by Pescador and Peters (1974).

The species can be distinguished from others of the genus by the following combination of characters. In the imagoes: (1) the basal 1/3 of the forewings and 3/4 of the hind wings are dark reddish-brown; (2) abdominal tergites 7-9 have anterior marginal black bands; and (3) the penes are lanceolate, apically blunt, and gradually enlarged basally (fig. 2i). In the nymph: (1) frontal projections are prominent, strongly bifid, and extend almost to the level of the anterior margin of the head (fig. 11a); (2) genae are greatly flared, broad and angulate (fig. 11a); (3) mesonotal shield has serrated, sharp-pointed spines (fig. 11a); (4) dorsal projections of the
mesonotal shield are prominent, ranging from being less than to subequal to the height of the medial hump (fig. 7d); and (5) abdominal sternites 7-9 have a pair of prominent brownish-black spots.

_Baetisca rogersi_ appears to be most closely related to _B. becki_ but can be distinguished from it by any of the following characters. In the imagoes: (1) basal 1/3 of the forewing and basal 3/4 of the hind wing is dark reddish-brown; (2) abdominal tergites 7-9 have an anterior, marginal black band. In the nymph: (1) thoracic sterna and abdominal sternites 2-6 lack distinct markings: (2) lateral margins of the mesonotal shield are both crenulate and serrate (fig. 11a); (3) lateral spines of the mesonotal shield are approximately 1.3 times as long as wide at base, and basal 2/3 is pronouncedly serrate along the margins (fig. 11a); (4) dorsal projections on mesonotal shield are distinctly less than or subequal to the height of the medial hump (fig. 7d); and (5) markings on abdominal sternites 7-9 are characterized by a pair of brownish-black spots.

_Biology and Ecology._ — A recent review of the family Baeticidae (Berner and Pescador, 1980) includes a brief summary of the ecology and life history of _B. rogersi_. The nymphs are found in gravel or stony beds with moderately swift to fast flowing streams (Berner 1940, 1950; Pescador and Peters 1974). The nymphs are detritivores and development requires 12 instars. Nymphs occur from September through July and adult emergence begins in March and extends through early July. The species is univoltine (Pescador and Peters 1974).

_Specimens Examined:_ ALABAMA: _Barbour Co:_ 23 VI 54 (N) (FSCA). _Escambia Co:_ Panther Cr, near Bradley, 30 I 71 (N), 17 IV 71 (N, A reared), 21 II 75 (N), 26-29 III 77 (N), 10 VI 77 (N, A reared), 11 XI 78 (N), 15 XII 78 (N) (FAMU), Perdido Cr, 3 VI 40 (N) (FSCA), Perdido R, 28 IV 67 (N) (FAMU). FLORIDA: _Bay Co:_ Bear Cr near Panama City, 27 I 54 (N) (FAMU), Little Bear Cr, near Youngstown, 28 IV 67 (N) (FAMU), Pine Long Cr, 5 V 71 (N) (FAMU). _Calhoun Co:_ Chipola R, 12 IV 72 (N) (FAMU). _Escambia Co:_ Pine Barren Cr, 27 I 68 (N) (FAMU). _Gadsden Co:_ Bear Cr, 8 V 67 (N), 5 I 68 (N), 10 III 68 (N), 5 V 68 (N, A reared), 14 IX 68 (N), 4 V 69 (N, A reared), 7 II 74 (N), 9 V 74 (N), Rocky Comfort Cr, 12 I 67 (N), 8,15 X 67 (N), 19 XI 67 (N), 15 XII 67 (N), 5, 31 I 68 (N), 11-28 II 68 (N, A reared), 3, 24-29 III 68 (N, A reared), 1, 5, 12 V 68 (N, A reared), 6 IX 68 (N), 25 X 68 (N), 23 XI 68 (N), 18, 28 XII 68 (N), 1 II 69 (N), 4-29 III 69 (N, A reared), 2-19 IV 69 (N, A reared), 11, 19 IV 69 (N, A reared), 4-25 V 69 (N, A reared), 15 VII 69 (N), 6, 9 XI 70 (N), 3, 22 I 70 (N), 10, 15 II 70 (N), 18 III 70 (N), 1, 12 IV 70 (N),
27 X 71 (N), 10 XI 71 (N), 11 IV 72 (N), 12 XI 73 (N), 4-26 I 74 (N), 20, 28 II 74 (N), 14 III 74 (N), 3-22 IV 74 (N, A), 16 II 75 (N), 12 V 76 (N) (all preceding specimens FAMU), Ocklawaha Cr, south of Quincy, 9 IV 67 (N), 27 VI 77 (N) (FAMU), Mosquito Cr, 30 XI 60 (N)._okloosa Co: Blackwater R near Holt, 10 IV 70 (N), 30 I 71 (N), 14 IV 77 (N), Blackwater R, FAMU Biol. Sta., 15-17 IV 71 (N), 3-8 VI 72 (N, A), 12-21 IV 73 (N), 21 IV 74 (N, A reared), 4 V 74 (N), 19 III 77 (N), 20, 23 IV 77 (N, A reared), 6-7 V 77 (A), 29 III 78 (N), 12 XI 78 (N), Blackwater R near Good Hope, 28 IV 72 (A reared), 15 XII 78 (N), Blackwater R near Blackman, 25 X 69 (N), 11 IV 70 (N, A reared), 1 V 70 (N), 25 IV 71 (N, A), 27-29 IV 72 (N), 1-8 V 73 (N, A reared), 28 IV 73 (N), 16 II 74 (N), 3 V 74 (N), 7 IV 77 (N), 11, 21 XI 78 (N), 15 XII 78 (N), Blackwater R near Cannon Town, 26-29 IV 67 (N), 20 V 67 (N), 10 VII 67 (N), 7 IV 68 (N), 26 VI 69 (N), 11-12 IX 69 (N), 12 IV 70 (N), 29 I 71 (N), 21 II 71 (N), 15, 29 IV 77 (N), Blackwater R at Fla. Hwy 4, 9 III 60 (N), Blackwater R near Baker, 27 XI 68 (N), 13 III 71 (N), Juniper Cr, 11 II 54 (N), 1 III 60 (N), Live Oak Cr, Eglin AFB, 21 XI 70 (N), Penny Cr, 11 XI 78 (N), Shoal R, Dorcas, 2 V 70 (A), Cr near Niceville, Fla Hwy. 285, 8, 11 III 60 (N), Sweetwater Cr, 9 III 60 (N), 16 VIII 60 (N), Titi Cr, Eglin AFB, 22 XI 70 (N), Turkey Hen Cr, 21 XI 70 (N), Yellow R near Holt, 8 III 66 (N), Yellow R near Oak Grove, 25 IV 67 (N). Santa Rosa Co: Blackwater R near Harold, 29 IV 67 (N), 19 V 67 (N), 28 VI 68 (N), Blackwater R at Riley Bluff, 11 II 72 (N), 8, 27 IV 72 (N), Juniper Cr near Munson, 16 XI 68 (N), Big Juniper Cr, 6 III 76 (N), 4 V 77 (A), East Fork Big Coldwater Cr, 22 VII 72 (N), Rileys Cr, 23 V 73 (N). Walton Co: Alaqua Cr, 6 XI 70 (N), 12 I 71 (N), 19 VI 71 (N), 14 II 72 (N). Walton Co: Black Cr, Eglin AFB, 7 XI 70 (N), Black Cr near Bruce, 28 III 71 (N), 14 XII 70 (N), 13 I 71 (N), 2 V 71 (N), Gum Cr near Defuniak Springs, 24 IV 67 (N, A), Lafayette Cr, Eglin AFB, 8 XI 70 (N), 12 I 71 (N), 27 I 72 (N) (all preceding specimens FAMU). GEORGIA: Cherokee Co: Etowah R near Ball Ground, 22-25 VI 71 (N) (FAMU). 20 VI 56 (N) (FSCA). Decatur Co: Mosquito Cr, 28 III 54 (N) (FSCA). Peach Co: Mossy Cr, 10 IV 54 (N) (FSCA). SOUTH CAROLINA: Aiken Co: Upper Three Runs Cr, 21 III 79 (N), 31 III 79 (N), 19 IV 79 (N), 5 VI 76 (N) (CU), Jackson-Hollow Cr, 20 IV 79 (N) (CU). Lexington Co, 2 IV 55 (N) (FSCA). Oconee Co: Little R near Salem, 5-7 V 72 (N, A reared) (FAMU), Chattooga R at state line, 26 VI 71 (N) (FAMU).

**Baetisca** (Baetisca) *rubescens* (Provancher)

Figures 2i, 14a,b, 15a)

*Cloe unicolor* Hagen; Provancher 1876:267; 1877:84
*Cloe rubescens* Provancher 1877:82; 1878:267
*Baetis rubescens* (Provancher); Eaton 1885:169
*Baetisca rubescens* (Provancher); McDunnough 1921:118; Traver 1931:45; Needham, Traver, and Hsu 1935:562; Berner 1950:147; 1959:8; Edmunds, Jensen, and Berner 1976:272; Berner and Pescador 1980:518.

**Male Imago** (in alcohol and dried). — *Length*: body 5.0-6.0 mm; forewing 6.0-7.0 mm; caudal filaments 4.5-5.5 mm.

**Head**: Dark reddish-brown. Scape and pedicel of antennae reddish-brown, flagellum brown, progressively paler distally. Eyes almost contiguous dorsally.
Thorax: Dark reddish-brown on anterolateral margins of mesonotum; apex and lateral surface of mesoscutellum blackish-brown. Sterna brown, reddish-brown around coxae.

Wings: Longitudinal veins of forewing brown, crossveins colorless except light brown near base and cubito-anal areas; membrane hyaline, basal 1/3 and costal and subcostal membranes of forewing, and almost entire hind wing flushed with orange-brown, hind wing darkest at base becoming progressively lighter distally.

Legs: Yellowish-brown, coxae reddish-brown; dorsum of tarsal claws brown, venter pale yellowish; protarsal segments with narrow reddish-brown band.

Abdomen: Terga reddish-brown; tergites 2-6 slightly darker than others; gill scars and posterior margins of terga dark reddish-brown. Sterna yellowish except sternites 2 and 3 brownish-yellow. Genital forceps yellowish. Penes yellowish, lanceolate, apically blunt, gradually enlarged basally (fig. 2i). Caudal filaments pale yellow; inconspicuously light brown annulations at articulations, progressively faded distally.

Female Imago (in alcohol and dried). — Length: body 5.5-6.5 mm; forewing 8.5-9.0 mm; caudal filaments broken except in dried specimens (strongly curled).

Head: Color and markings as in male except for presence of black margins on vertex.

Thorax: Color and markings as in male.

Wings: Color and markings as in male.

Legs: Color as in male except for lack of bands on protarsal segments.

Abdomen: Color and markings as in male imago; sternite 9 shallowly cleft, depth approximately 1/10 maximum width of sternite.

Mature Nymph (in alcohol). — Length: body 8.0-11.0 mm; caudal filaments 2.0-3.0 mm.

Head: Brownish-yellow with reddish-brown tubercles. Frontal projection weakly developed, truncate (fig. 14a). Genal spines developed, short with upcurved brown tip barely visible when viewed dorsally (fig. 14a). Antennae brownish-yellow.

Thorax: Mesonotal shield broad, ratio of length to width measured from base of lateral spines 1.03:1.0; anterolateral and lateromedial lobes smooth and weakly developed (fig. 14a), lateral spine short, shorter than width at base (fig. 14a), apically blunt; dorsal projections weakly developed, lower than median hump; posteromedian dorsal depression shallow and broad (fig. 4b). Mesonotal shield brownish-yellow with small reddish-brown tubercles and linearly and obliquely arranged reddish-brown mottling (fig. 14a); lateral margins finely crenulate. Sterna brownish-yellow with some brown mottling, mostly between coxae.

Legs: Brownish-yellow, claws shiny brown, femora with small reddish-brown tubercles, tibiae and tarsi with light-brown median band, more pronounced on tarsi.

Abdomen: Tergites 7-10 and posterior 1/2 of tergite 6 brownish-yellow with small reddish-brown tubercles; dark-brown markings on tergites 7-9, spots on mid-posterior margin linearly arranged forming broken median longitudinal line; lateral margins of segments 6-9 crenulate. Sterna brownish-yellow with reddish-brown mottling (fig. 14b). Posterolateral projections on segments 6-9 weakly developed, longest on segment 9; posteromedian elevation on tergites 7-9 weakly developed,
largest on 9 extending approximately 1/5 length of tergite 10. Caudal filaments brownish-yellow, dark brown in basal half.

**Variations:** We noted few nymphal variations among the limited number of specimens available to us. One nymph from Vermont has a pair of solid, oblique, longitudinal bands on tergites 7-9, the remainder have linearly arranged dark brown spots. The nymphs generally are brownish-yellow, but two nymphs from Maine are almost entirely dark reddish-brown with the exception of the base of the genital spine, unbanded areas of the legs, and the apical 1/2 of the caudal filaments, which are greenish-yellow. Similarly a few nymphs from Maine have more numerous dark-brown spots on abdominal tergites 7-9 than the remainder which were collected from the same locality as well as other areas.

**Geographical Distribution:** *Baetis rubescens* has been collected only in the northeastern section of North America from New Hampshire to Quebec (fig. 15a).

**Discussion.** — The species was first described under the name *Cloe unicolor* Hagen by Provancher (1876) but recognized by him as a new species, which he named *Cloe rubescens* a year later. Eaton (1885) subsequently assigned the species to *Baetis*, and McDunnough (1921) transferred it correctly to *Baetisca*.

The type locality of *B. rubescens* was not given and Eaton assumed that it was probably Quebec. It is likely that Eaton was correct as adult specimens have been collected subsequently in Laprairie, Quebec, by Ide in 1924 and in St. Lambert by G.S. Walley and W.J. Brown in 1927. In 1928 Brown also collected specimens of *Baetisca* (6 mature nymphs, 2 nyphal exuviae, and 1 female imago) in Knowlton, Quebec, which were identified as *B. carolina* by Traver. The specimens are actually *B. rubescens*. The female imago is the same as the ones from Laprairie and St. Lambert except that it has a larger body size. The size difference could be the result of later emergence. Variability in size among adults of *B. rogersi* due to difference in date of emergence has been observed by Pescador and Peters (1974) and it would not be surprising to find the same types of differences occurring in other members of the genus. Adults of *B. rogersi* emerging early in the season are generally larger than those emerging late in the season.

Similarly the nymphs collected in Knowlton are *rubescens* and not *carolina*, as indicated on Traver's determination label. As pointed out elsewhere, the nymphs are distinctly different morphologically from *B. carolina*. Although association of nymphs and adults of the same species for geographical reasons alone is not a good practice, we feel confident in doing so in this particular
case. Mature nymphs, nympha! exuviae, and the female imago were collected in the same locality and on virtually the same date.

*Baetisca rubescens* can be distinguished from the other species of the genus by the following combination of characters. The imagoes have (1) the basal 1/3 and almost the entire costal and subcostal membrane of the forewing and the entire hind wing flushed with orange-brown; (2) the posterior margins of the abdominal terga are reddish-brown; and (3) the penes are lanceolate, apically blunt, and gradually enlarged basally (fig. 2i). In the nymphs: (1) the frontal projection is weakly developed (fig. 14a); (2) the genal spines are short and barely visible when viewed dorsally, upcurved and sharp pointed at the tip (fig. 14a); (3) the lateral margins of the mesonotal shield are finely crenulate and the lateral spines are short and blunt, being almost as long as the width at the base (fig. 14a); (4) the dorsal projections on the mesonotal shield are weakly developed and lower than the median hump (fig. 4b); and (5) the abdominal sterna have variable markings as discussed above.

The imagoes of *B. rubescens*, according to Traver (1935), differ from *B. carolina* in being smaller, having orange-flushed wings, and darker legs. We found, however, that body size and leg color are unsuitable characters for differentiating the two species.

*Baetisca rubescens* can be separated from the closely related *B. bernerri* and *B. carolina* by the following combination of characters. In the imagoes: (1) basal 1/3, and entire costal and subcostal membranes, of forewings, and entire hind wings are faintly flushed with orange-brown; and (2) penes are gradually enlarged basally (fig. 2i). In the nymph: (1) genal spines are barely visible when viewed dorsally (fig. 14a); (2) spot between genal spines and eyes is absent; and (3) mesonotal shield has short and blunt lateral spines which are as long as the width at the base (fig. 14a).

**Biology and Ecology.** — Except for the collection records of mature nymphs in June and adults in July, the biology and ecology of the species is unknown.

Baetisca (Fascioculus) escambiensis Berner

Figures 2g, 8b,d,e, 12b, 15a


Male Imago (in alcohol). — Length: body 9.5-10.0 mm; forewing 10.5-11.5 mm; caudal filaments 8.5-9.0 mm.

Head: Red-brown markings present below eyes, extended ventrally; median carina and area below antenna deep brown. Antennal scape purplish-brown, remainder of segments brown. Eyes almost contiguous dorsally.

Thorax: Pronotum brownish with brown median line extended throughout entire length of segment; membranous areas purplish. Mesonotum brown, mottled with lighter color, deepest brown medially; base of scutellum with two large submedian oblong, brown marks; remainder pale with margins outlined in dark brown. Prosternal process deep brown. Mesosternum shiny brown; metasternum paler brown.

Wings: Longitudinal veins of fore- and hind wings tinged with dark reddish-brown; membrane of fore- and hind wings flushed with ruby, more intense along costal margin and between veins R₁ and R₂ of forewing; brownish tinge at extreme base of both wings; crossoveins in anterior 1/2 of hind wing margined with pale areas giving appearance of blocks of deeper ruby color between crossoveins.

Legs: Brown, distal ends of femora and tibiae slightly darker; tarsal segments with narrow, dark-brown band at joints.

Abdomen: Terga dark brown; intersegmental membrane giving purplish cast to posterior border of each tergite; remnants of gill attachments purplish-brown; tergites 2-5 with faint, submedian, pale line; tergites 6-10 with deep-brown, median line; tergite 6 with submedian, triangular, pale areas followed by a large, butterfly-shaped, brown area with large pale blotches in outer portions; posterior 1/2 of tergite 6 with large triangular area with apex at midpoint of tergite and base of posterior border; lateral to median line on tergites 7-10 lighter brown area; brown mottling toward lateral margins of segments. Sternites brownish with purplish tinge, becoming more intense towards lateral margin; middle portions shaded with purplish-red, more intense laterally; sternites 7 and 8 with large, pale, median, triangular area with base on posterior margin of sternites and apex extending almost to middle of sternite. Genital forceps brown along outer margins, inner margins pale. Penes brown, sharply tapered near apex (fig. 2g). Caudal filaments brown.

Female Imago. — Unknown. Examination of the female subimago indicates color pattern similar to that of male. Forewing length of female subimago 14.0-15.5 mm.

Mature Nymph (in alcohol). — Length: body 10.0-13.0 mm; caudal filaments 2.5-3.0 mm.

Head: Yellowish, tuberculate with tubercules most prominent near base of genal spines; margins with long hairs. No frontal projection present. Genal spines well developed, long, flat, slightly upcurved at the deep-brown tip; clearly visible and prominent both dorsally and ventrally (fig. 12b). Antennae pale.
Thorax: Thorax compressed dorsoventrally. Mesonotal shield broad with ratio of length to width 1.4-1.5:1.0; anterolateral and lateromedial lobes weakly developed (fig. 4a); lateral spines approximately 2-1/2 times as long as width at base, slightly recurved, sharp pointed (fig. 12b); dorsal projections absent (fig. 4b); strongly carinate median ridge running length of mesonotal shield, deeply notched near posterior border. Mesonotal shield with conspicuous deep-brown marks, two laterals with one close to anterolateral corner, other slightly posterior to first, third pair of dark-brown marks adjacent to median line forming V-shaped marking about middle of mesonotum. Sterna pale, except in middle of mesosternum and anterior part of metasternum which are brownish. Thorax bordered with long hairs.

Legs: Pale, unbanded. Hairy, clusters of hairs at base, densest on trochanters and femora; tibiae and tarsi without hairs.

Abdomen: Tergites 7-10 and anterior 1/2 of tergite 6 brown; tergites 7-10 with median longitudinal brown line; tergites 7 and 8 with pale rectangular area, mottled with brown at lateral margins; segments 6-8 with long hairs along lateral margins as well as being serrate; short hairs on margins of segments 9 and 10, 9 also serrated. Posterolateral projections on segments 6-8 well-developed, flared outwards and sharp pointed (fig. 12b); posteromedian elevations on tergites 7-9 well developed, upturned. Sternites 3-6 pale with light-brown mottling anterolaterally. Caudal filaments light brown.

Variations: In younger nymphs, genal and lateral mesonotal spines and abdominal posterolateral projections are more accentuated than in mature specimens.

Geographical Distribution: The species is known only from extreme northwestern Florida and southeastern Mississippi (fig. 15a).

Discussion. — Both nymphs and adults of B. escambiensis are so distinctive that they cannot be confused with any other species of the genus. The imagoes have: (1) wings flushed throughout with a ruby tint and the eyes are banded with vertical stripes; (2) the abdominal terga are dark brown with the intersegmental membranes purplish giving an annulated appearance to the abdomen; and (3) the penes are uniquely shaped, being sharply tapered distally (fig. 2g). The nymphs have: (1) no frontal projection (fig. 12b); (2) the genal spines are well-developed, long, flat, and with the deep-brown tip slightly upcurved (fig. 12b); (3) the mesonotal shield is compressed dorsoventrally and has a strongly carinated median line; (4) there is no dorsal projection on the mesonotal shield; and (5) the lateral margins of the body are covered with long hairs (fig. 12b).

Biology and Ecology. — Nymphs inhabit sand bars in small to medium sized rivers. They have been found in "shallow water from four to five inches up to one foot in depth, where they lay partially buried in the stream bed . . . Where they were most abundant,
there was also an admixture of clay in the sand. The current was relatively slow, in some places there was a growth of algae over the bottom." (Berner 1955, p. 7). The streams of northwestern Florida from which nymphs were collected have a yellowish to whitish shifting sand bed and they are generally rather shallow. The nymphs rest on the and but are partially covered by soft, silty deposits so that only a small part of the insect is visible.

Relatively few male and female adults have been collected or reared. Adults emerge very late in the year, as indicated by our collections and rearings of the nymphs, with all our records being from the end of October to late November. Although we have succeeded in having 17 female subimagos emerge successfully from the nymphal stage, none has molted to the imago. Of the males which emerged, nine failed to undergo the final molt while six completed it. We have five adult males which were collected in the field. Emergence may take place from mid-morning to early afternoon. The subimaginal stage requires 40-44 hours in the laboratory. Apparently females emerging in the laboratory have great difficulty in molting to the adult stage as indicated by our failure to raise one successfully.

Our evidence shows that *B. escambiensis* is univoltine with emergence occurring only very late in the year.


**Phylogenetic Relationships and Zoogeography of The Genus *Baetisca***

*Baetisca* species possess a number of morphological and ecological characters which, when carefully analyzed, make it possible to group the species into phylogenetic units exhibiting various degrees of specialization. Construction of the phylogeny, as discussed here, was based primarily on nymphal characters with only a few adult characters complementing the nymphal data. Like
most mayflies, *Baetisca* adults are morphologically homogeneous with relatively little differentiation between species. Derivation of character states is based on the concept that ancestral character states are generally widespread in the genus and often in the family and order.

Figure 14c shows our interpretation of phylogenetic relationships of the species of *Baetisca*. The sequence of branching is based on shared possession of derived character states.

Furcation 1 represents the common ancestral derivation of subgenera *Baetisca* s.s. (Lineage 1A) and *Fasciocolus* (Lineage 1B). Interesting evolutionary changes occurred between these two lineages after splitting from a common ancestor. Within the subgenus *Fasciocolus* (Lineage 1B), there has been the development of striped eyes in both nymphs and adults as well as sharply tapered penes (fig. 2g), long hairs (fig. 12b), and dorsoventrally compressed mesonotal shield, all of which represent derived character states (Table I). Additionally, *Fasciocolus* nymphs differ ecologically and behaviorally from *Baetisca* s.s. as they generally inhabit streams and rivers with shifting sand beds and are commonly found partially buried in silty deposits. Conversely, *Baetisca* s.s. nymphs mostly live in stony streams or those with an admixture of gravels, or in sand-bottom streams and rivers. The development of long hairs and a dorsoventrally compressed mesonotal shield among *Fasciocolus* nymphs apparently help them become adapted to the type of environments in which they live. The long hairs very likely serve to protect the nymphal integument from being heavily coated with silty deposits, and the dorsoventrally compressed mesonotal shield seems to aid the nymphs in maintaining their position in seemingly unstable habitats.

Furcation 2 represents the first major split within the subgenus *Baetisca* s.s. Lineage 2A (*B. becki, B. berneri, B. carolina, B. gibbera, B. rogersi, and B. rubescens*) underwent varied genal development ranging from broadly produced and strongly flared (fig. 10b) to sharply pointed, upcurved spines (fig. 10d). Lineage 2B (*B. lacustris, B. laurentina, and B. obesa*), on the other hand, retained the ancestral, slightly produced and rounded genal shelf (fig. 13b).

Progressive development of nymphal genae into sharp-pointed, upcurved spines clearly defines Lineage 3B (*B. berneri, B. carolina,
and *B. rubescens* from Lineage 3A (*B. becki*, *B. gibbera*, and *B. rogersi*). Lineage 3A retained the ancestral genal development (Table I, Fig. 10b). It is tempting to speculate that the genal spines perhaps are an adaptation to fast-flowing mountain streams. Nymphs in Lineage 3B are most common in the Appalachian mountain streams (fig. 15a) while those in Lineage 3A are mostly Coastal Plain residents, except for *gibbera* which extends its distribution to the Appalachian mountain region. *Baetisca* nymphs are positively rheotactic and perhaps the genal spines offer an effective streamlining effect as an adaptation to living in fast flowing mountain streams.

Massive broadening of the nymphaal mesonotal shield (length subequal to width) coupled with the shortening of lateral spines (length subequal to width and mostly blunt) separate *B. gibbera* (Lineage 4A) from sister species *B. becki* and *B. rogersi* (Lineage 4B) which retained the ancestrally less massive mesonotal shield and longer lateral spines (Table I, fig. 11a), and a prominent pair of dorsal projections (fig. 10a). Adult *B. gibbera* lost their imaginal wing color which is retained in *B. becki* and *B. rogersi*.

Nymphs of *B. berneri* and *B. carolina* (Lineage 5A) retained their sharp-pointed mesonotal lateral spines which are blunt in *B. rubescens* (Lineage 5B). Adult male *Baetisca rubescens*, however, do have lanceolate penes (fig. 2i) which is an ancestral trait compared to the derived, ovate penes found in *B. berneri* and *B. carolina* (fig. 2j).

Elongation of the mesonotal shield and development of dorsal projections represent some of the evolutionary changes separating *B. lacustris* (Lineage 6A) from sister species *B. laurentina* and *B. obesa* (Lineage 6B). *Baetisca lacustris* nymphs have a comparatively broad mesonotal shield (Table I, fig. 13a), and greatly reduced dorsal projections (fig. 4b). Mesonotal shields of *B. laurentina* and *B. obesa* are elongated (length more than 1-1/2 times the width) and they have well-developed dorsal projections (fig. 13c). Except for the difference in penes shape, which is lanceolate in *B. obesa* (fig. 2i) and deltoid in *B. lacustris* and *B. laurentina* (fig. 2h), adults of these three closely related species are morphologically indistinguishable.

It is clear that the genus *Baetisca* is restricted in its distribution to
that part of North America lying east of the Continental Divide and associated with the drainage pattern of the Mississippi River. No specimens, to our knowledge, have been taken from the southwestern United States. Two collections, which are suspect, have been reported from extreme western North America. Our doubts related to *B. columbiana* are discussed under that species. Eaton's listing (1885, p. 229) of *B. obesa* from California cryptically states, "... California (MaLach. Mus.)" with no other information. His other records of the occurrence of *B. obesa* are consistent with our findings. We feel that Eaton's record from California is in error and we reject the assumption that *Baetisca* occurs there. In support of this contention, we feel that in the nearly one hundred years since his report someone would have taken another specimen, especially such assiduous collectors as Richard K. Allen or the late Willis Day.

Interestingly, the proposed phylogeny of the species correlates nicely with their geographical distribution and closely related species have very similar distributional patterns (fig. 15).

The most highly restricted species is *Baetisca escamibiensis*, which is known only from extreme northwestern Florida. The most widely distributed species group includes *B. lacustris, B. laurentina*, and *B. obesa*. Both *B. lacustris* and *B. laurentina* occur widely in Canada and in the central plains and southeastern regions of the United States (fig. 15b). The closely related *B. obesa* has a similar geographical distribution, except that it is not known from Canada.\(^2\)

*Baetisca bernerii, B. carolina*, and *B. rubescens* occur in the generally cool mountain streams of the Appalachian System (fig. 15a). Both *B. bernerii* and *B. carolina* are found in the mountains of the southeast with a slight northeast extension for the former species (fig. 15a). *Baetisca rubescens* is presently known only from the extreme northeastern United States and southeastern Canada (fig. 15a), and both areas are part of the Appalachian System (King 1977).

---

\(^2\)Lehmkuhl (1972, p. 1015) reported *B. obesa* from Saskatchewan and Alberta; however, his photograph of the nymph is clearly that of *B. laurentina*.
Baetisca becki, B. gibbera, and B. rogersi occur in the Coastal Plain section of the southeast (fig. 15c), except for B. gibbera which has also been collected from the mountain streams of Virginia, and West Virginia (fig. 15c).

The distributional pattern of Baetisca offers some interesting possibilities. Lehmkuhl (1972) speculated about the causative factors determining the distribution of B. lacustris (= B. bajkovi) and B. laurentina. According to him, all of the northern range of these two species, including the entire Hudson Bay System, was covered by ice ten to twelve thousand years ago so that colonization from the ice-free areas of the south, which served as a refugium, was necessary. As the ice receded, rivers which served as dispersal routes from the United States refugium for invasion to the north have changed their direction of flow and have isolated populations in the Hudson Bay drainage from the parent population in the Mississippi drainage. In other words, B. lacustris and B. laurentina moved northward from the parental population in the Mississippi drainage after the Pleistocene ice sheet retreated.

It is not inconceivable to assume that the generally cool-water adapted B. bernerii, B. carolina, and B. rubescens represent a group that was either pushed into or trapped in the ice-free streams of the Appalachians during the Pleistocene glaciation. Since then, the group has remained in the cool mountain streams. The disjunctive distribution of B. rubescens from sister species B. bernerii and B. carolina could very well be due to separation of aquatic links of the central Appalachian with streams of the extreme northeastern United States, or simply to lack of adequate collections.

The species now occurring in the extreme southeastern United States (B. becki, B. escambiensis, B. gibbera, B. rogersi, and perhaps B. obesa) represent the group that was pushed southwards by the glaciation and remained adapted to warmer water temperatures. B. gibbera is the exception as it also occurs in the cool mountain streams of the Appalachian mountains (fig. 15c). The disjunct distribution of B. gibbera could possibly be the result of an insufficient number of collections or the mountain population may prove to be a distinct species. If the species is not distinct, then the distributional pattern indicates that B. gibbera became adapted to cool waters and invaded the streams of the Ap-
palachians as the ice sheet receded while continuing to be an inhabitant of the warmer coastal streams.

The large number of *Baetisca* species in the southeastern United States seems to indicate that much speciation has occurred in the area, especially in the warm waters of the Coastal Plain, Florida, with six species reported from its northern region, has the greatest variety of species within its boundaries. Perhaps as other areas of the continent are subjected to careful scrutiny they, too, will show the diversity that is apparent here. As is often the case, geographic distribution of a species simply reflects the presence in an area of interested collectors.

Speculation about the origin of the diverse Florida fauna leads us to the conclusion that the boreal endemic genus *Baetisca* (Edmunds et al., 1976) was pushed southward during the Pleistocene glaciation. With the receding of the ice sheet, the streams of northwestern Florida provided ideal conditions for speciation resulting in the comparatively large number of *Baetisca* species in the area. The species known to occur in the Florida panhandle are *B. becki*, *B. escambiensis*, *B. gibbera*, *B. laurentina*, *B. obesa*, and *B. rogersi*.

Lack of comprehensive studies of the biology and ecology of most species of the genus hinder an in-depth analysis of their historical biogeography.

**REFERENCES**

*Includes only those papers not listed in Berner and Pescador, 1980 (Part I).*

---


