

**RECENT DISCOVERIES IN THE *BLEPHARICERA TENUIPES* GROUP,
INCLUDING DESCRIPTIONS OF TWO NEW SPECIES FROM
APPALACHIA (DIPTERA: BLEPHARICERIDAE)**

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ABSTRACT. Two new species of *Blepharicera* (*B. appalachiae* and *coweetae*) are described in the *Blepharicera tenuipes* group. Both occur in the southern half of the Appalachian Mountains in eastern North America, the former of wide distribution, the latter restricted to a small portion of the upper Little Tennessee drainage. A key to all the known stages in the *B. tenuipes* group is provided along with new information on ecology, distribution, and phylogeny (for which the sister *Blepharicera micheneri* group is newly recognized).

INTRODUCTION

At the time of his review of the net-winged midges of eastern North America, Hogue (1978) preferred not to make definite identifications of the immatures of any species because of the uncertainty of stage associations until better material could be acquired. He was also unable to distinguish more than one pupal type. The recent availability of numerous specimens, including some valuable individual rearings, collected in the vicinity of the United States Forest Service's Coweeta Hydrologic Laboratory (Macon County, North Carolina) by Georgian and associates, has now made it possible to separate pupae of five of the eastern species. Using integumentary characters of this intermediate stage, we can also identify several of the larvae by inspection of prepupal larvae and pharate adults.

These integumentary characters include the patterns and detailed structures of the papillae and cuticular ornamentation of the abdominal tergites. Streams in the Coweeta locality produce two very distinctive pupal types, the adults of which show small, but consistent features that distinguish them from existing species. They are considered new species and are described here.

Other discoveries in the *Blepharicera tenuipes* group also are presented. Complete synonymies are reserved for a monographic treatment of the Blephariceridae of North America soon to be published (Hogue, in press).

MATERIALS AND METHODS

MATERIALS

Most of the new material used for this study was collected by T. Georgian and D.H. Ross, and placed in the University

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of Georgia Entomological Museum and the Entomology Section of the Natural History Museum of Los Angeles County. However, some paratypes are deposited in the U.S. National Museum of Natural History. See the Acknowledgment section for explanations of abbreviations used for sources of other specimens.

A number of larvae and adults of *B. appalachiae* were considered by Hogue (1978) as a variant of *B. tenuipes* (Walker, 1848). These specimens have been reevaluated and some identifications modified. All those that are now determined as belonging to the new species are listed here; the others cited in that paper as "Atypical adults" (p. 23) and "Larva E" (p. 30) are still of uncertain identity.

TERMINOLOGY

The terminology used in this paper is mostly that established in Hogue's (1978, 1981) earlier treatments of blepharicerid anatomy. One important change is the application of the name "*lateral tine*" to the prong-like, tubular rods lateral to and paralleling the aedeagal filaments and which have been called "parameres" in most previous works on the family. The tines appear to be secondary developments of the ventral plate (whose presence is probably plesiomorphic for the family) as proposed by Stuckenberg (1958:101). They are represented either by (1) no more than mere pigmented straps, or (2) as columnar projections without a lumen. The first case occurs in *Blepharicera micheneri* and its close relatives in western North America; the second is the condition in *Paltostoma*, as seen in Hogue's (1979) figures of Costa Rican species. Blepharicerid tines are possibly homologous to similar structures given the same name in the terminalia of tabanids by Bonhag (1951:161, 198).

The neutral term "*gonites*" is used here for the large, wide plates subtending and sometimes surrounding the base of the

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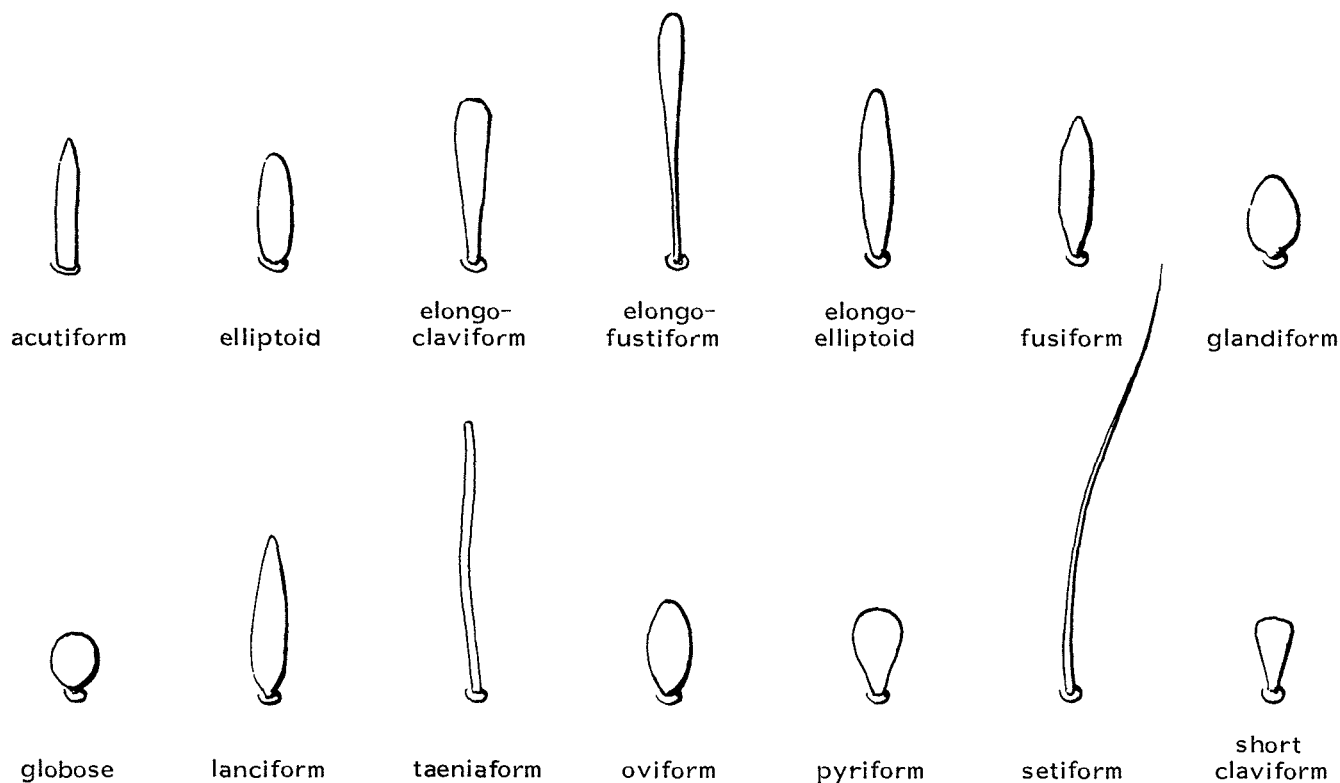


Figure 1. Various forms taken by the modified, dorsal secondary sensilla of the larvae of the *Blepharicera tenuipes* group. Names as used in descriptions.

aedeagus that have been also called "parameres" by authors (McAlpine, 1981:51f). According to G.C.D. Griffiths (pers. comm.), the latter term should be reserved presently for quite distinct organs in other insect orders and not applied to the Diptera until controversies in homologies can be settled.

Leg segment proportions are expressed "progressively," that is, each segment is compared to its proximal neighbor rather than to one standard segment (customarily the most basal segment).

The various forms taken by the modified (generally short, peg-like), dorsal secondary sensilla of the larvae are described with adjectives whose precise definition can be appreciated by the shapes labelled in Figure 1 (only those displayed by species included in this paper are given). See Hogue (1978) for designations of primary setae.

MEASUREMENTS

All measurements are made from topotypic material, unless otherwise noted, and cited in millimeters. The first value represents the mean of the number of specimens indicated by N; values following in parentheses are range extremes. Larval body length is taken only on prepupal specimens (i.e., those showing some trace of pupal branchiae). Adult proboscis length is approximate, measured from a point level with the venter of the eyes to the apex of the labella. The

formula for expressing comparative sizes of male vs. female pupae is (L)(W) male/(L)(W) female. Meristic counts of sensilla are cited for one side of bilateral structures as absolute values "(20)" or ranges "(15-20)"; where it is necessary to cite different values for each side, a double parenthetical notation is used "(5)(15)".

Blepharicera tenuipes Group

PHYLOGENY

With the addition of the two new species described in this paper the *Blepharicera tenuipes* group contains eight species, all restricted in geographic occurrence to the eastern United States (Appalachians, northward to Hudson's Bay and Labrador, westward to eastern Minnesota). We consider them very closely related and all descended from a single ancestor, as did Hogue (1978).

It has not yet been possible to arrive at a clear phylogeny of the species within the group, because of their homogeneity and incongruous variation in many characters. These blepharicerids are so alike morphologically that relatively few synapomorphies can be distinguished, except one found in the male terminalia. Also, a reticulate pattern of the following synapomorphies emerges when they are applied toward construction of a cladogram:

1. Inner margin of the Xth tergite lobe convexly expanded medially. A simple, straight inner margin is the plesiomorphic condition.

2. A slight to well-developed apicomedial, dorsal carina present on the tegmen. The plesiomorphic tegmen is flat apically.

3. Apex of lateral tine with a conspicuous recurved hook. A simple apex is plesiomorphic but other autapomorphies are common.

4. Apex of tegmen strongly emarginate on either side of median carina. The plesiomorphies entire to weakly emarginate, may actually be reduction apomorphies correlated with small size in those species with this condition. The deep emargination nevertheless is a strongly positive apomorphy.

5. Median aedeagal filament decidedly heavier than laterals.

6. Many integumentary papillae of pupal tergites occurring in diads. These papillae are normally more or less evenly spaced on the sclerites.

Most of the species are closely related to and similar to *tenuipes*, judging from the common shape of the Xth tergite lobe (quadrate with distinct triangular apical sublobe). This configuration may be considered plesiomorphic to the type found in *williamsae* Alexander, 1953, *capitata* Loew, 1863, and *similans* Johannsen, 1929, that have a greatly expanded medial margin, and therefore not a reliable state for indicating relationships. Among these latter three species, the heavy (synapomorphic) median aedeagal filament would seem to indicate a close relationship between the first two, but the very different *similans* could have closer affinities with the *tenuipes* cohort than with the other two species because of its somewhat more similar Xth tergite lobe. Among the species clearly similar to *tenuipes*, *cherokea* Hogue, 1978, and *diminutiva* Hogue, 1978, segregate by their smallness, a dubious synapomorphy when reduction in size can occur often in this midge family. Complicating the picture still more is the presence of a fairly strong apical carina on the tegmen in *williamsae* which relates it toward *tenuipes* and its close relatives, but away from *capitata*. Among the latter, *appalachiae* and *tenuipes* seem closely related on the basis of the common occurrence of irregular diad formations in the patterns of integumentary papillae on the pupae.

Therefore, at this stage of knowledge of the *Blepharicera tenuipes* group, we refrain from attempting a cladogram. More analysis of characters is needed before a clear selection of phylogenetically significant states can be ascertained. The possibility of hybridization between species may also have affected their evolution. Ultimately, it may be necessary to resort to chromosomal or biochemical analyses to detect interrelationships.

ZOOGEOGRAPHY

Zwick (1984) proposed a preliminary phylogeny of the genus *Blepharicera*. He considered the species of the western United States (with the exception of *B. ostensackeni*, here called the "*Blepharicera micheneri* group"), the sister group to the *B. tenuipes* group. The ancestral stock of both groups probably

arrived in North America from Asia because most *Blepharicera* reside there. The single European species belongs to a distinct group. This hypothesis conflicts with Hogue's earlier (1978:1-2) supposition of a fundamental division between the two stocks. He suggested that the former arrived in North America from the northwest, while the latter dispersed separately, and probably earlier, over an eastern connection with the Palearctic Region.

Zwick's arguments are convincing. The problem remains, however, of connecting the two lines paleogeographically, i.e., to answer the question, by what route did the *B. tenuipes* group reach eastern North America from the northwest? Also, what disruptive events forced the separation of the two groups?

Only a northern path across the Canadian Shield would seem a plausible answer to the first question, because a southern highland corridor was present no later than the Permian. It is unlikely that the *Blepharicerini* would have evolved before that time. Invasion of North America and movement eastward could have been associated with the mid-Cenozoic spread of the temperate deciduous forests, as supposed by Ross (1956) for various mountain caddisflies, such as the "Rhyacophila Siberica Group" (and "Wormaldia Anilla Group," and subgenus *Doloclanes*—p. 181-182), with distributions identical to or concordant with the *Blepharicera* in question. Baumann (1975) also noted similar patterns in some rheophilic stoneflies (*Podmosta*). A newly discovered montane genus of limnephilid caddisfly bears very strong affinities to western forms and is believed to have dispersed across the northern deciduous forest and undergone subsequent speciation in the Appalachians (Huryn and Wallace, 1984). The absence of *Blephariceridae* from the Ouachita and Ozark mountains, remnants of that intervening orogenic zone, and which surely would preserve some vestige of any past *blepharicerid* fauna, also provides evidence, albeit negative, in favor of the northern alternative.

The absence of a continuous east-west mountain chain along which these generally monticolous midges could have dispersed does not preclude the hypothesis of a northern route. *Blepharicera tenuipes* extends over low postglacial terrain in southeastern Canada, indicating the ability of these insects to colonize rapidly well-watered land with little relief. The distance between the most southern extreme of the Wisconsin ice sheet across Appalachia and the northernmost recorded Recent occurrence of the species is approximately 1500 km. The ice sheet began retreating from its terminal position about 15,000 years ago (Davis, 1983), giving the flies a dispersal rate of at least 0.1 km per year. To traverse the distance from the Rocky Mountains to the Appalachian Mountains (3500 km) would require about 35,000 years, an easy march, geologically speaking.

Increasingly arid conditions in the late Cenozoic undoubtedly forced the division of the eastern and western groups.

In North America, the greatest variety of species is concentrated in the southern Appalachian Highlands, particularly in the Blue Ridge area, an acknowledged important center of speciation and a refugium from glaciation (see the various papers listed in Holt, 1969). Although *Blephariceridae* are poorly vagile insects, three species (*B. tenuipes*, *sim-*

ilans, and *capitata*) dispersed considerable distances northward in the postglacial era. This seems to show that the adults can move across drainage boundaries fairly easily. Stream capture, while a common phenomenon in the geologic history of the area and significant for the dispersal of strictly aquatic organisms, is not their only means of colonization of new watersheds. However, *diminutiva* may have entered the Savannah drainage from the Little Tennessee when Stekoa Creek diverted the southern portion of the latter (south of Rabun Gap, Georgia) (Ross, 1971:32). The restricted distributions of *cherokea* and *coweetae* to the Little Tennessee (Ohio drainage) and northward indicates their probable origin subsequent to this stream-capture event.

TAXONOMY

The *Blepharicera tenuipes* group was defined by Hogue (1978: 6-8) on the basis of the adult flies. A more complete description and definition will appear in Hogue (in press). Zwick (1984) demonstrated some new diagnostic features, in particular some correlated states in the mesosomal complex of the male terminalia, namely, the short, heavy lateral tines, small apodeme of the sperm pump, and anteriorly expanded gonite from which arises a large muscle narrowly inserting at the base of the aedeagal tine and lateral to which the outer aedeagal filament passes. In the *B. micheneri* group this muscle passes lateral to all the aedeagal filaments, which are much reduced in size. The former arrangement is an autapomorphy for the group.

Identification of larvae in the group is somewhat problematical. The following keys only apply to typical specimens in the mature, fourth instar. Atypical larvae may show a considerable variety of conditions of the shape and distribution of the dorsal, secondary sensilla which are the primary identifying characters. There are many intermediates and non-conformants (species appearing to be out of their range or associated with stages of distinct species) and these cannot be assigned with certainty to any species. Therefore, many of the larval records cited by Hogue (1978) are suspect. Only detailed biological work with these Diptera can hope to shed light on the causes and significance of larval variability. Introgression among the closely related members of the group is suspected.

KEY TO ADULT MALES

(Based on the terminalia; slide mounts normally required to see structures)

- 1a. Medial aedeagal filament distinctly longer than laterals and with asymmetrical, hooked apex. Apex of lateral tine incurved, asymmetrically bifurcate. Outer corner of Xth tergite lobe slightly obtusely angulate, inner margin shallowly convex *similans*
- b. Medial aedeagal filament about same length as laterals and with simple apex. Apex of lateral tine not bifurcate. Shape of Xth tergite lobe varied 2

- 2a. Medial aedeagal filament distinctly thicker than laterals. Inner margin of Xth tergite lobe convexly expanded 3
- b. Medial aedeagal filament similar to laterals. Inner margin of Xth tergite lobe straight 4
- 3a. Inner wall of lateral tine incurved, apex acute and extending well beyond aperture. Inner margin of Xth tergite lobe expanded angularly to or beyond midline. Larger species, wing length 4.9-6.6 mm *williamsae*
- b. Inner wall of lateral tine very slightly produced, truncate, with a minute, pointed, dorsal projection, aperture terminal. Inner margin of Xth tergite lobe expanded evenly and moderately, far short of midline. Smaller species, wing length 4.8-5.3 mm *capitata*
- 4a. Apex of tegmen deeply incised on either side of strong, medial dorsal carina. Tip of lateral tine complex, with dorsally recurved, stout hook (Figs. 5, 9) 5
- b. Apex of tegmen weakly incised or entire on either side of weak, medial dorsal carina. Tip of lateral tine simple 7
- 5a. Interlobular space (between Xth tergite lobes) U-shaped (Fig. 8) 6
- b. Interlobular space V-shaped (Fig. 8) *coweetae*
- 6a. Posteromedial triangular sublobe of Xth tergite lobe situated midway along posterior margin *tenuipes*
- b. Posteromedial triangular sublobe of Xth tergite lobe displaced nearly to inner corner (Fig. 4) *appalachiae*
- 7a. Posteromedial triangular sublobe of Xth tergite lobe conspicuous, well produced; outer corner of lobe obtusely rounded *cherokea*
- b. Posteromedial triangular sublobe of Xth tergite lobe minute and barely produced; outer corner of lobe acutely rounded *diminutiva*

KEY TO ADULT FEMALES

(Slide mounts required to see details of terminalia; wing lengths given for confirmation)

- 1a. Two spermathecae, medial reduced to a narrow cylindrical rod. Wing length 5.4-7.3 mm *similans*
- b. Three spermathecae 2
- 2a. Ducts of lateral spermathecae sclerotized for a short distance before genital aperture. Wing length 5.2-6.4 mm *capitata*
- b. Ducts of spermathecae membranous throughout ... 3
- 3a. Scutum with a contrasting, light brown, quadrate area anterior to scutellum. VIIIth sternite lobe of terminalia devoid of setae. Spermathecae spherical. Large species; wing length usually 7.2 mm or greater *williamsae*
- b. Scutum generally unicolorous. VIIIth sternite lobe of terminalia usually with several setae, at least one. Smaller species; wing length 7.1 mm or less 4
- 4a. VIIIth sternite lobes of terminalia contiguous, medial depression V-shaped. Very small species; wing length about 5.1 mm *diminutiva*
- b. VIIIth sternite lobes of terminalia disjunct, medial depression U-shaped. Larger species; wing length 5.5 mm or greater 5

Note: Remaining species very difficult to distinguish. Following continuation of key is for typical specimens only. Wing lengths overlap.

- 5a. Accessory gland narrow throughout, apparently (one specimen available) sclerotized and pigmented anteriorly *cherokea*
- b. Accessory gland widened at some point, unpigmented throughout 6
- 6a. Accessory gland very wide posteriorly, twice narrowed anteriorly. Lobe of hypogynial plate apically truncate *tenuipes*
- b. Accessory gland moderately wide posteriorly, narrowing once anteriorly. Lobe of hypogynial plate variously shaped 7
- 7a. Anterior portion of accessory gland straight, parallel-sided. Lobe of hypogynial plate broadly rounded apically *appalachiae*
- b. Anterior portion of accessory gland dilated. Lobe of hypogynial plate narrowly rounded *coweetae*

KEY TO PUPAE

(Pupae of *capitata*, *diminutiva*, and *cherokea* unknown)

- 1a. Integument of abdominal tergites with a fine, reticulate pattern (Figs. 20, 25); surface dull. Larger (length usually 5.5 mm or greater) *williamsae*
- b. Integument of abdominal tergites homogeneous or otherwise sculptured, no reticulate pattern; surface shiny. Smaller (length usually less than 5.5 mm) 2
- 2a. Integument of abdominal tergites showing minute wavy furrows between and connecting the papillae. Papillae minutely spinulate (Figs. 18, 22) *coweetae*
- b. Integument of abdominal tergites between papillae uninterrupted by cuticular furrows or lines. Papillae smooth 3
- 3a. Papillae, especially in region lateral to muscle scars of abdominal tergites clustered, unevenly distributed, often arranged in pairs or diads (Figs. 12, 17, 21, 24) 4
- b. Papillae all more or less evenly spaced (Figs. 19, 23) *similans*
- 4a. Frequent papillar diads in medial zone of abdominal tergites (between muscle scars) as well as lateral (Figs. 17, 21) *appalachiae*
- b. Papillae of median zone of abdominal tergites all more or less evenly spaced (Figs. 12, 24) *tenuipes*

KEY TO LARVAE

(Larvae of *capitata*, *cherokea*, and *diminutiva* unknown. Larva "F" (Hogue, 1978) apparently an aberration of other species; see below)

- 1a. Dorsal secondary sensilla mostly setiform (Fig. 13) (taeniaform to elongo-fustiform³ in many specimens) *appalachiae*

3. Latin: *fustis* = cudgel + *forma* = shape.

- b. Dorsal secondary sensilla mostly modified (capitate to claviform) present dorsally 2
- 2a. Modified sensilla large, globose, apically spinulate, clustered in vicinity of st and tp primary sensillae and anteromedially on segment (Fig. 15) *similans*
- b. Modified sensilla small to medium, mostly elongate forms, apically smooth, clustered or diffusely arranged 3
- 3a. Modified sensilla short claviform to pyriform, arranged generally in transverse anterior and posterior clusters, the latter including primary sensillum st (Figs. 10, 11) *tenuipes*
- b. Modified sensilla more or less generally distributed over segment (may be in broad transverse patterns but never clustered) 4
- 4a. Modified sensilla lanciform to fusiform, arranged in 3 broad transverse fields medially (Fig. 16). Dorsum longitudinally dark pigmented medially, light laterally ... *williamsae*
- b. Modified sensilla pyriform, glandiform or oviform, diffusely distributed (Fig. 14). Dorsal pigmentation uniform *coweetae*

DESCRIPTIONS OF NEW SPECIES

Blepharicera appalachiae, new species

Figures 2-5, 13, 17, 21, 26

Blepharicera tenuipes "Atypical (southern type)" of Hogue, 1978:21, fig. 24.

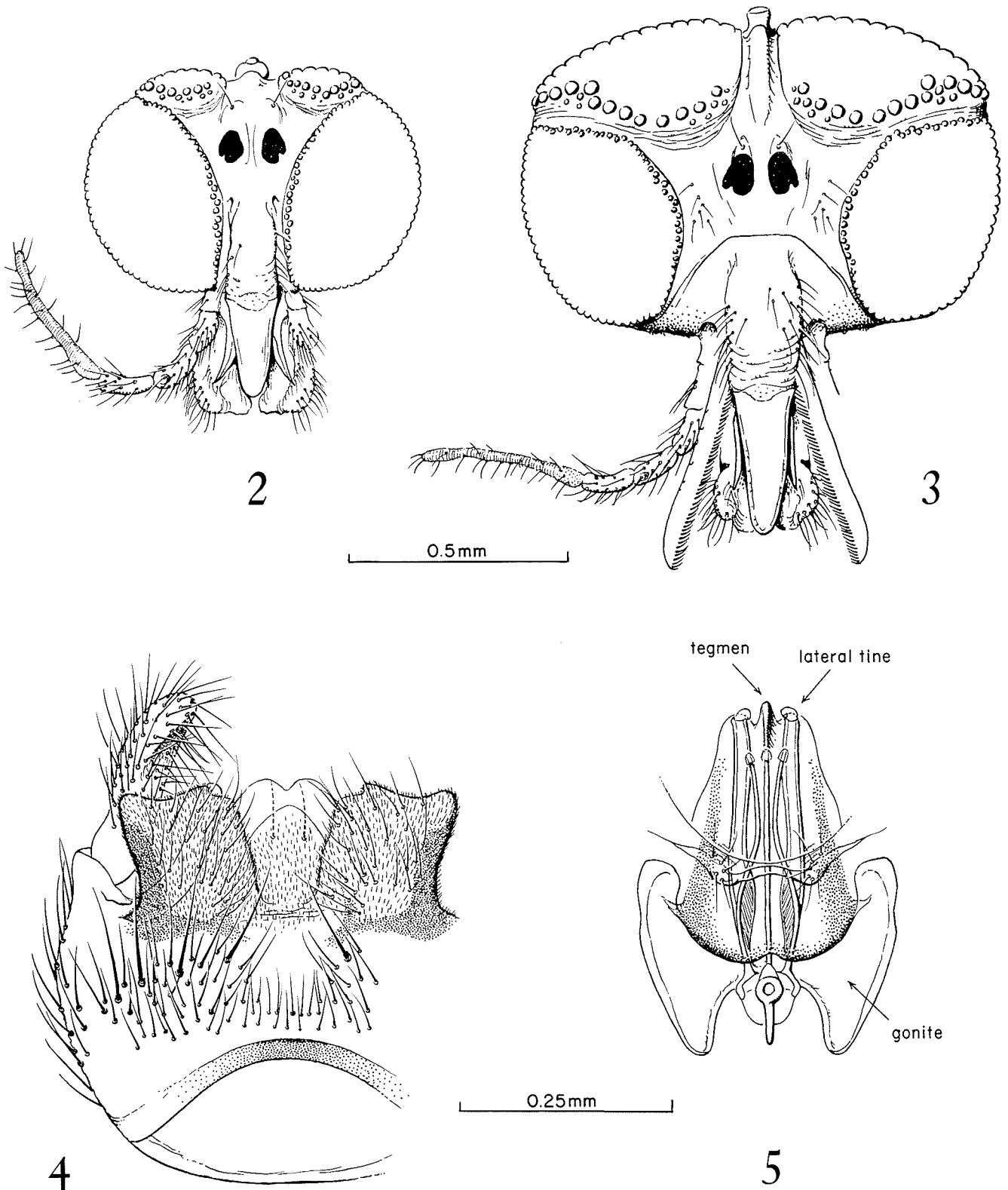
Larva "E" (partim) Hogue, 1978:29-30.

Larva "C" Hogue, 1978:28-29, fig. 35.

DIAGNOSIS. In the male terminalia, while all structures are otherwise virtually identical to those of *B. tenuipes* and other members of the *B. tenuipes* group, the posterior margin of the Xth tergite lobe is uniquely shaped: the outer corner is acutely rounded, followed medially by a deep concavity and central sublobe strongly displaced toward the inner corner. The secondary sensilla on the larval dorsum are typically setiform rather than peg-like or otherwise modified, as in *tenuipes* and other members of the group. (A few modified sensilla may intrude in some specimens.) The arrangement of the dorsal papillae distinguishes the pupa. The papillae are very irregularly arranged, neighboring pairs often coalescing into diads over the entire surface of the abdominal tergites, but more so in the outer areas lateral to the main muscle scars.

DESCRIPTION. Adult a small, sturdily built, well-sclerotized blepharicerid. Very similar to *B. tenuipes* and *coweetae*.

Male (Figs. 2, 4-5). *Coloration.* Generally dull gray-brown, pruinose. Mesoscutum concolorous, dull gray. (With illumination at some angles, lateral portions become translucent, reddish-brown, medial area longitudinally brown to blackish.) Corners of posterior pronotum and scutellum contrasting light brown, pleurites similar to scutum. Wing membrane completely hyaline. *Size.* A medium-sized *Blepharicera*.



Figures 2-5. *Blepharicera appalachiae*, new species. 2. Male head. 3. Female head. 4. Male terminalia, external structures (dorsal view). 5. Male terminalia, phallic structures (dorsal view).

Measurements (from non-topotypical material) (N = 10):
Wing length 5.3 (5.0–6.0). Leg segment lengths:

	foreleg	midleg	hindleg
femur	3.2 (3.1–3.7)	3.4 (3.2–3.9)	4.6 (4.3–5.1)
tibia	3.0 (2.9–3.3)	2.9 (2.8–3.3)	4.3 (4.0–4.8)
tarsus 1	1.6 (1.5–1.8)	1.5 (1.4–1.7)	1.7 (1.5–1.9)
2	0.80 (0.76–0.89)	0.74 (0.66–0.81)	0.53 (0.46–0.62)
3	0.55 (0.51–0.64)	0.52 (0.48–0.57)	0.35 (0.29–0.42)
4	0.29 (0.27–0.36)	0.29 (0.27–0.34)	0.24 (0.22–0.29)
5	0.29 (0.27–0.32)	0.29 (0.27–0.34)	0.28 (0.25–0.33)

Head (Fig. 2). Structure: Normal type, subholoptic. Suprafrontal carina a rounded convexity. Clypeus elongate, L/W = 2.0. Eyes approximate dorsally, interocular distance equal to combined diameters of 5 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi narrow), much smaller (0.4×) than lower in area, 10–11 rows of ommatidia along mid-meridian; upper ommatidia slightly larger (1.4×) than lower in diameter. Proboscis short, free portion about 0.4× head width; mandibles completely absent; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.3–3.4. Antenna 15-segmented, flagellar segments elongate throughout, ultimate longer (1.4×) than penultimate, apical 3 segment proportions 1.0–1.0–1.4. Sensilla: Setiform groups on head capsule as follows: clypeals several (10), medium, only a few, small setae medially, more numerous and longer along distolateral margins. A single, medium strong seta over antennal socket; facial groups otherwise absent. Postocellars few (2–3), small, lateral. Medioccipitals absent. Supracervicals very numerous (30), tiny. Occipitals separated from and larger than postgenals, numerous (30), long. Postgenals numerous (17–26), smaller toward center of group.

Thorax and appendages. Structure: Wing venation typical for *Blepharicera*. Tibial spurs 0–0–1. Progressive leg-segment proportions: foreleg 0.9–0.6–0.5–0.7–0.6–0.9; midleg 0.8–0.5–0.5–0.7–0.6–1.0; hindleg 0.9–0.4–0.3–0.7–0.7–1.1. Sensilla: Macrotrichia on wing veins as follows: complete ventrally on R₄ and dorsally on R₅; apicodorsally only on M₁, M₂, and CuA₁. Setiform groups on thoracic sclerites as follows: anterior pronotals apparently absent. Humeral callus with 4–5 small setae. Acrostical series short. Dorsocentral series apparently absent. Supraalars few (6–7), restricted to posterior and medial portions of sclerite. Prescutellars several (6). Scutellars medium-sized, forming a dense group on outer corner, numerous, similar, more widely spaced setae dispersed toward the midline. Metapleurals absent. Suprametapleurals few (3–4), small.

Terminalia (Figs. 4–5). Structure: Abdominal segment VIII greatly reduced, mostly membranous; tergite consisting of a short, medial, ligulate sclerite, sternite and pleurites undifferentiated. Epandrium simple, emarginate posteromedially. Xth tergite lobes well developed, prominent, parallel; interlobular depression deep, U-shaped; individual lobe shape quadrate, apex trilobate: outer sublobe acutely rounded; middle sublobe small, displaced toward inner corner, also slightly angled inwardly; inner sublobe right-angled; inner margin

straight, paralleling outer and extending directly to base of lobe; distal margin of lobe between outer and middle lobes slightly concave; inner arm poorly sclerotized, elongate, apex lobate, disjunct from same member opposite. Fused gonocoxites and hypandrium well sclerotized, forming capsule about as wide as long; posterolateral corners of gonocoxite strongly produced. Outer gonostylus large (length about 0.7× mid-line length of hypandrium), an entire, subrectangular, lobe with concave inner margin. Inner gonostylus a narrow, correct, smooth, simple, digitiform projection. Phallic complex straight, supinate, not recurved. Aedeagal filaments equal, with slightly flared apices, outer filaments strongly bowed outward near bases; lateral tine longer than rods, broad throughout, tapering slightly to complex apex; latter with dorsal hook on inner wall; canal wide toward the base and containing numerous long spiculae, arising from inner wall and directed toward the apex; aperture subapical. Sperm pump and piston poorly developed, former without internal spines, latter with conspicuous, tubular ejaculatory atrium attached to apodeme; apodeme a small, ventral, vertical flange. Subanal pouch wide, bowl-shaped; tegmen broad, apex trilobate: deeply incised on either side of strong, vertical, medial carina. Gonite large, broad, ovate; gonocoxal lobe poorly developed, posterior lobe elongate, anterior lobe expansive, ventral bridge complete beneath basiphallus. Sensilla: Epandrium with numerous, short to long setiforms generally, these shorter toward the anterior. Xth tergite lobe with medium setiforms generally and evenly spaced over central portion dorsally these longer toward the apex; inner arm with few to several (5–8), small setiforms near apex. Fused gonocoxites and hypandrium ventrally with numerous, medium setiforms, these spaced generally only over posterior half. Outer gonostylus with very numerous, medium setiforms generally and evenly spaced over outer surface and marginally, absent from middle of inner face. Epiproct with few (4–6) alveoliforms in dorsolateral group. Hypoproct with few (3–4) long setiforms apically.

Female (Fig. 3). Coloration and measurements from non-topotypic material. **Coloration.** As in male, paired medial longitudinal lines present under some illumination. **Size.** A medium-sized *Blepharicera*. Measurements (N = 6): Wing length 6.7 (6.2–7.6). Leg segment lengths:

	foreleg	midleg	hindleg
femur	3.8 (3.6–4.2)	3.8 (3.4–4.2)	5.3 (4.9–5.8)
tibia	3.2 (2.9–3.5)	3.2 (2.9–3.5)	4.8 (4.4–5.3)
tarsus 1	1.6 (1.5–1.7)	1.5 (1.4–1.7)	2.1 (1.9–2.3)
2	0.78 (0.72–0.82)	0.77 (0.71–0.81)	0.72 (0.65–0.78)
3	0.49 (0.44–0.54)	0.51 (0.46–0.55)	0.45 (0.38–0.52)
4	0.34 (0.29–0.38)	0.32 (0.28–0.37)	0.32 (0.28–0.38)
5	0.40 (0.37–0.42)	0.40 (0.36–0.44)	0.40 (0.36–0.44)

Head (Fig. 3). Structure: Normal type, subholoptic. Suprafrons narrow, with a long, strongly convex carina. Clypeus elongate L/W = 2.5. Eyes approximate dorsally, interocular distance equal to combined diameters of 1–2 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi very broad, anterior portion strongly striate), approximately equal to lower in area, somewhat flattened

dorsally, 15–16 rows of ommatidia along mid-meridian; upper ommatidia much larger ($2.3\times$) than lower in diameter. Parietal sclerite broad, trapezoidal in outline shape. Proboscis short, free portion about $0.6\times$ head width; mandibles present and complete; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–2.4. Antenna 15-segmented, flagellar segments narrowly elongate throughout, ultimate longer ($2.0\times$) than penultimate, apical 3 segment proportions 1.0–0.9–1.7. Sensilla: Setiform groups on head capsule as follows: clypeals numerous (23–24), medium, only a few small setae medially, these more numerous and longer along distolateral margins. A single, moderately strong seta over antennal socket. Parietal setae several (5–7 usually, rarely more, 14–16). Postocellars few (2–3), small, lateral. Medioccipitals absent. Supracervicals numerous (23–25), tiny. Occipitals separated from and larger than postgenals, numerous (18), long. Postgenals numerous (14–15), smaller toward center of group.

Thorax and appendages. Structure: Wing venation as in male. Tibial spurs 0-0-2 (inner twice length of outer). Hind basitarsus short. Progressive leg segment proportions: foreleg 0.8–0.5–0.5–0.6–0.7–1.2; midleg 0.8–0.5–0.5–0.7–0.6–1.3; hindleg 0.9–0.4–0.4–0.6–0.7–1.3. Sensilla: Macrotrichia of wing veins and setiform groups on thoracic sclerites as in male.

Terminalia. Structure: Posterior margin of VIIIth sternite lobe broadly bilobate, medial depression shallow; sclerotization in base of latter rectangular (much wider than long). Hypogynial plate subquadrate, base slightly wider than apex; with weak transverse creases across base; apex broadly rounded (outer angle not distant from level of tip). Accessory gland elongate, posterior sides subparallel (not dilated anteriorly). Spermathecae 3 in number, equal in size and shape, ovoid; necks very short; ducts completely unsclerotized. Sensilla: Medial group of VIIIth sternite with several to numerous (7–20, usually more than 15), small setae; posterior lobe with several (7–10), medium setae dispersed generally. Short, stout apicodorsal setae of hypogynial lobe several to numerous (9–20). Epiproct with 2 apical setae. Alveoliforms of hypoproct few (4–6).

Pupa (Figs. 17, 21). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral third), scutellar, and abdominal tergites densely papillose. Individual papillae smooth, rounded, oval convexities. Pattern disperse, papillae unevenly spaced, often arranged in pairs or diads (some confluent), both in central area of abdominal tergites and areas lateral to muscle scars. Cuticle between papillae uniform in structure. *Coloration.* Surface reflection shiny; pigmentation more or less even throughout. *Size.* Medium. Measurements, male ($N = 48$): body length 4.1 (3.5–4.7), width 2.5 (1.9–2.7); female ($N = 26$): body length 4.7 (3.9–5.2), width 2.9 (2.3–3.2); male about $0.7\times$ size of female. *Structure.* Outline shape almost ovoid, L/W male = 1.7, female = 1.6; cross section convex, sides declivous all around. Dorsal sclerites: abdominal tergite margins symmetrically convex, of II and

III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about $0.3\times$ length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost coterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular secutate in outline.

Larva (Fig. 13). *Integument.* Dorsally with distinct, but fine, linear and zigzagging corrugations, these absent ventrally. *Coloration.* Trunk evenly pigmented, medium-brown, sclerotized portions dark brown to black. *Size.* Medium for the group. Measurements ($N = 20$): body length 5.9 (4.7–7.1), head capsule width 1.24 (1.14–1.41), antennal segment lengths, basal 0.12 (0.11–0.15), apical 0.18 (0.17–0.21). *General shape.* Cylindrical. *Head.* Antenna short, 2-segmented, intersegmental membrane wide; segment proportions 1.0–1.45. *Trunk.* Structure: Anterior division spheroid. Lateral margins of abdominal segments inclinous, truncate (pseudopods extending well beyond); dorsopseudopodal lobes small and poorly developed. Anal division trilobate: lateroterminal lobe acutely rounded; pleuron straight, medioterminal lobe truncate posteriorly; terminal incision shallow, widely V-shaped. Sensilla: Primary trunk sensilla: tP submedial, taeniaform, tM–T submedial, small, taeniaform, tI–VII submedial, taeniaform, stP lateromedial, taeniaform, stM–T lateromedial, elongo-elliptoid, stI lateromedial, elongo-fustiform, stII–VII lateromedial, large, setiform. Inner tpP far-lateromedial, disjunct from stP, setiform, inner tpI–VII far-mediolateral, disjunct from and anterior to stI–VII, large, setiform. Outer tpI–VII near and slightly lateroposterior to inner tp, smaller, setiform. pdpodI–VII indiscernible. Inner and outer dpodM–T proximate, those of M sublateral, of T mediolateral, setiform, dpodI–VII on minute, anterolateral tubercle (= dorsopseudopodal lobe), setiform, inner and outer dpodVIII contiguous, at apex of lateroterminal lobe, setiform. ssP slightly lateral to ssM–T, decidedly larger than latter. Dorsal secondary trunk sensilla: numerous, more or less generally distributed, usually all setiform with a few taeniaform to elongo-fustiform types intermingled. Terminal setae 3-3, marginal.

VARIATION. Larval specimens are common in which a few or most of the central dorsal sensilla are modified (elongo-fustiform, elongo-pyriform to subclaviform, larval type “C,” of Hogue, 1978:fig. 35). These are probably referable to *appalachiae* and some are confirmable as that species by the presence of pharate pupal structure observable beneath the cuticle. It might be theorized that these represent individuals in which introgression is occurring from other regional species which normally have modified setae (*williamsae*, *coweetae*). Further analysis of large samples and reared material are needed to explain these chaetotactic variations.

SPECIMENS EXAMINED. Types. HOLOTYPE male

(extracted from pupal skin), in alcohol with skin (terminalia and head dissected and mounted on slides nos. CLH 84-35 and 84-94, respectively): NORTH CAROLINA, *Macon County*. Coweeta Hydrologic Laboratory, Lower Shope Fork, 9 May 1981, T. Georgian (LACM).

ALLOTYPE female (extracted from pupal skin), in alcohol with skin (terminalia dissected and mounted on slide no. CLH 84-33): same locality and collector as holotype, 28 May 1982 (LACM).

Eight PARATYPE males and females (extracted from pupal skins) on slides and in alcohol, with skins: same locality and collector as holotype, 9 May 1981, 28 May 1982 (LACM, UGAM, USNM).

Additional specimens. GEORGIA, *Rabun County*. Betty's Creek: 23 March 1984, T. Georgian (37 larvae); 7 April 1984, T. Georgian (22 larvae, 6 pupae).

MARYLAND, *Frederick County*. Little Catoclin Creek, 1 mi. N Harmony, 30 May 1958, P.H. Freytag (1 pupa: OSU). 0.5 mi. E Yellow Springs, 31 May 1958, P.H. Freytag (1 larva, 8 pupae: OSU). Cunningham Falls State Park, Little Hunting Creek, 17 May 1984, R.W. Baumann and C.R. Nelson (2 larvae, 10 pupae: BYU).

NORTH CAROLINA, *Macon County*. Clear Creek, 3200 ft., Highlands, 2 July 1958, J.G. Franclemont (2 females: CU). Highlands, 3000–5000 ft., May 1936, R.C. Shannon (3 males: USNM). Coweeta Hydrologic Laboratory, Lower Shope Fork, 2300 ft., T. Georgian: 9 May 1981 (23 larvae, 5 pupae); 24 April 1982 (34 larvae, 29 pupae); 28 May 1982 (10 pupae); April 1984 (11 larvae). Dryman's Fork, 2100 ft., T. Georgian: 1 April 1980 (9 larvae); 21 April 1980 (25 larvae, 5 pupae); 21 April 1980 (3 larvae, 2 pupae). *Swain County*. Deep Creek, Great Smoky Mountains National Park, Bryson City, Deep Creek Campground, 21 May 1970, G.B. Wiggins and T. Yamamoto (1 pupa, 2 males: ROM).

TENNESSEE, *Sevier County*. Great Smoky Mountains National Park, Greenbrier Cove, 2000 ft., 22 May 1938, Williams (1 male: USNM). Great Smoky Mountains National Park, 18 May 1957, J.R. Vockeroth (1 male: CNC).

VIRGINIA, *Bath County*. Blowing Springs Camp, 8 mi. W Warm Springs, 18–20 May 1963, C.M. and O.S. Flint (2 males, 1 female: USNM). Wilson Creek, Route 629, 12 May 1979, C.R. Parker (3 males, 1 female: BCK). *Giles County*. Stoney Creek, 1800–2000 ft., 26 May 1962, J.R. Vockeroth (1 larva, 33 pupae: CNC). Sinking Creek, 29 May 1941, A. Stone (1 pupa: USNM). *Madison County*. Shenandoah National Park, White Oak Creek, 24 June 1951, B.D. Burks (4 larvae, 5 pupae: USNM). *Nelson County*. Crabtree Creek, Crabtree Falls, Highway 56, 28 May 1984, R.W. Baumann and C.R. Nelson (2 males, 1 female: BYU). *Page County*. Luray, 21–24 June 1933, A. Melander (2 males, 3 females: USNM). *Patrick County*. Confluence of Little Rock Castle Creek and Rock Castle Creek, Route 605, 31 May 1980, B. Kondratieff (1 male, 2 females: BCK). *Rockbridge County*. Pedlar River, below Panther Falls, 28 May 1984, R.W. Baumann and C.R. Nelson (9 males, 4 pupae: BYU). *Shenandoah County*. Passage Creek, Camp Roosevelt, 21 May 1973, S. Fiance (3 larvae: USNM). *Smyth County*. N Fork Holston

River, Route 42, junction Route 633, 9 May 1981, B. Kondratieff (1 male: BCK). *Washington County*. S Fork Holston River, Highway 58, near Damascus, 27 May 1984, R. Baumann and C.R. Nelson (2 pupae: BYU).

ETYMOLOGY. The name is considered a noun in the genitive case and refers to the southern Appalachian Mountains where the species is of wide occurrence.

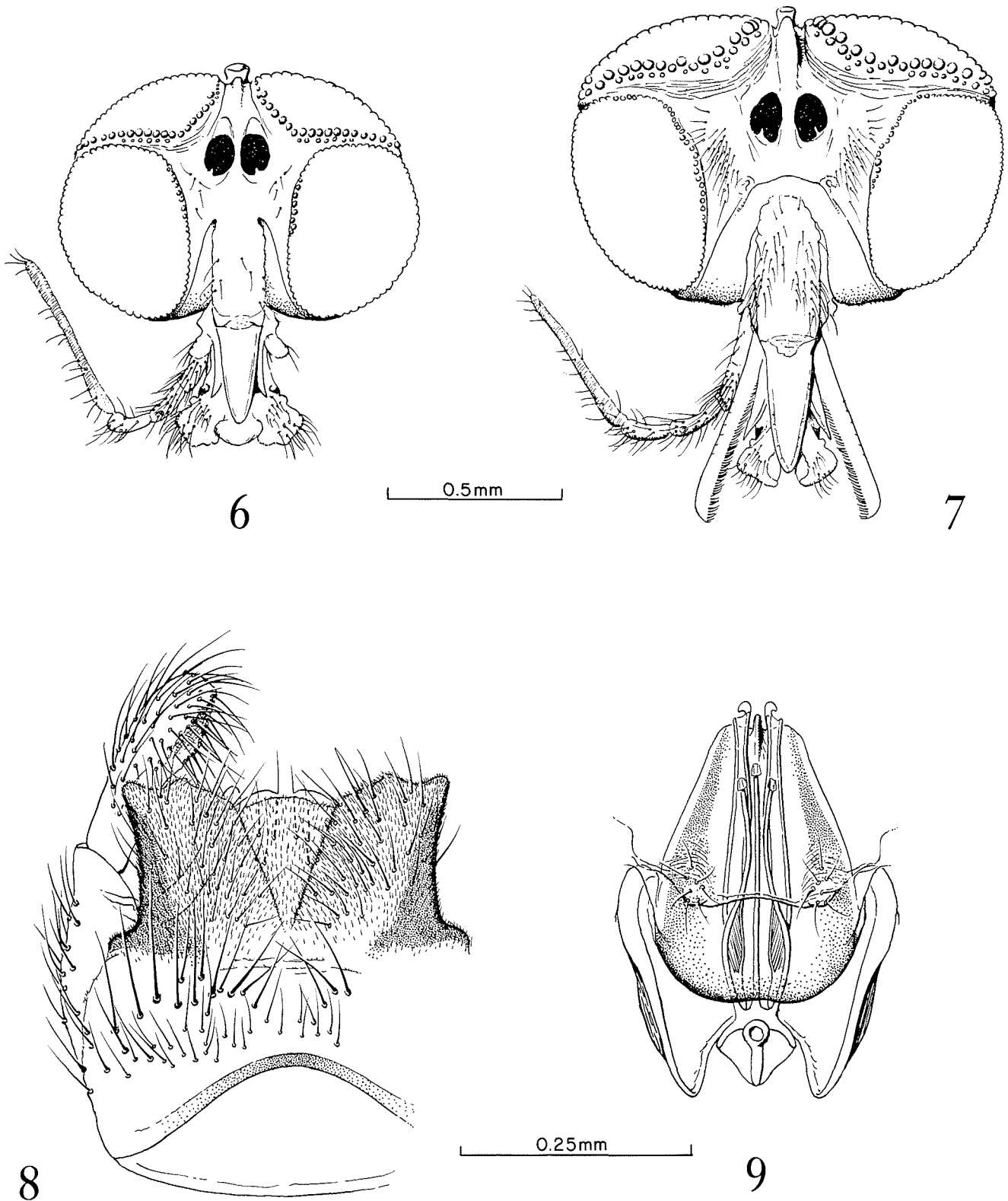
DISTRIBUTION. *Blepharicera appalachiae* is widespread in most major drainages throughout the central and southern Appalachian Mountains (Fig. 26). It is replaced largely by *tenuipes* to the north, except for a zone of overlap in Maryland and Virginia (to Giles County). Its distribution southward ends in northern Georgia (Rabun County), but it has not been found in the Savannah River drainage, although it is present less than 17 km away in the southernmost portion of the Little Tennessee system.

ECOLOGICAL NOTES. The larval ecology of *B. appalachiae* is similar to that of other members of the family (cf. Hogue, 1981). The stream at the type locality is a fourth-order mountain stream with average width 5.5 m, average velocity 50 cm/sec, and a bed predominantly of schist and quartzite boulders averaging 21 cm in greatest dimension. At least three other blepharicerid species (*B. coweetae*, *similans*, and *williamsae*) are also present. Some habitat segregation based on rock size and water depth has been observed (Georgian, unpubl. data), but individuals of more than one species have been collected from single rocks. The four larval instars can be identified by measuring the width of the dorsal head sclerite, permitting analysis of life cycles (Georgian and Wallace, 1983). Of the four species present at the Coweeta Hydrologic Laboratory, *B. williamsae* is the most abundant and the earliest to appear. Larvae are first seen in early winter (first instars December–March, mature larvae February–April or early May); they pupate in early spring (April–May). *B. appalachiae* and *coweetae* complete their larval development from early April through the end of May, and are much less abundant than *williamsae*. The last species to become evident in the annual cycle is *B. similans*, noticeable larvae appearing in early May, with pupae present throughout the summer until mid-September. The rate of growth and timing of life cycles changes with elevation (and is presumably controlled by correlated temperatures). At a site near the type locality only 490 m higher (Coweeta Hydrologic Laboratory, Watershed #27, 1158 m), mature larvae and pupae of *B. williamsae* were found and other species were absent as late as the first of June.

Blepharicera coweetae, new species

Figures 6–9, 14, 18, 22, 26

DIAGNOSIS. *B. coweetae* differs from other members of the *B. tenuipes* group in the unique shape of the Xth tergite lobe: outer corner acutely rounded, followed medially by a shallow concavity and central sublobe displaced toward the midline; the inner margin is straight but angled toward the midline so that the interlobular depression is V-shaped. The larva is most similar to that of *B. tenuipes* but is smaller,



Figures 6-9. *Blepharicera coweetae*, new species. 6. Male head. 7. Female head. 8. Male terminalia, external structures (dorsal view). 9. Male terminalia, phallic structures (dorsal view).

evenly pigmented, and has disperse, longer, predominantly fustiform dorsal sensilla whereas this stage of that species is much larger, usually with longitudinal light bands in the otherwise dark pigmentation and has short claviform dorsal sensilla in series. The pupa displays a unique pattern of light lines in the generally darkly pigmented integument, composed of numerous, very fine, closely set, longitudinal, narrowly wavy, transparent furrows and short, transverse "hyphens," the former appearing macroscopically as strong striae.

DESCRIPTION. Adult a small, sturdily built, well-sclerotized blepharicerid. Very similar to *B. tenuipes* and *appalachiae*.

Male (Figs. 6, 8–9). Only a single, freshly emerged, alcohol-preserved specimen (holotype) available for coloration and measurements; character values of latter may be insufficient due to incomplete development. Other structural characters from pharate adults dissected from pupae. *Coloration.* Generally dull gray-brown, pruinose. Mesoscutum unicolorous, dull gray, corners of posterior pronotum and scutellum contrasting light brown, latter becoming darker toward the sides; pleurites similar to scutum but paler. Wing membrane completely hyaline. *Size.* A medium-sized *Blepharicera*. Measurements (N = 1): Wing length 6.1. Leg segment lengths:

	foreleg	midleg	hindleg
femur	3.6	3.9	5.2
tibia	3.2	3.0	4.7
tarsus 1	1.8	1.6	1.8
2	0.91	0.83	0.66
3	0.64	0.60	0.44
4	0.33	0.32	0.28
5	0.32	0.33	0.32

Head (Fig. 6). Structure: Normal type, subholoptic. Suprafrons narrow, with long, moderately convex carina. Clypeus elongate, L/W = 2.0. Eyes approximate dorsally, interocular distance equal to combined diameters of 2.8 upper ommatidia; eye divided, upper division well differentiated from lower (callis oculi narrow), approximately equal to lower in area, 19–20 rows of ommatidia along mid-meridian; upper ommatidia slightly larger (1.5×) than lower in diameter. Proboscis short, free portion about 0.4× head width; mandibles completely absent; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–3.0. Antenna 15-segmented, flagellar segments elongate throughout, ultimate longer (1.4×) than penultimate, apical 3 segment proportions 1.0–0.9–1.25. Sensilla: Setiform groups on head capsule as follows: clypeals several (9–10), medium, only a few, small setae medially, more numerous and longer along distolateral margins. No single, medium strong seta over antennal socket; parietal setae few (1–2). Postocellars few (2–5), small, lateral. Medioccipitals absent. Supracervicals very numerous (30), tiny. Occipitals separated from and larger than postgenals, numerous (26–30) and long; upper series of longer and heavier setae than lower. Postgenals numerous (12–26), small toward center of group.

Thorax and appendages. Structure: Typical wing venation for *Blepharicera*. Tibial spurs 0–0–1. Progressive leg-segment proportions: foreleg 0.9–0.6–0.5–0.7–0.5–1.0; midleg 0.8–0.5–

0.5–0.7–0.5–1.0; hindleg 0.9–0.4–0.4–0.7–0.6–1.1. Sensilla: Macrotrichia on wing veins as follows: complete ventrally on R₄ and dorsally on R₅; apicodorsally only on M₁, M₂, and CuA1. Setiform groups on thoracic sclerites as follows: anterior pronotals absent. Humeral callus with 3 very small setae. Acrostical series short, divergent anteriorly. Dorso-central series complete. Supraalars few (5), restricted to posterior and medial portions of sclerite. Prescutellars absent. Scutellars medium-sized, forming a dense group on outer corner; numerous similar, widely spaced setae dispersed toward the midline. Metapleurals present, few (2–6). Suprametapleurals 2–3, minute.

Terminalia (Figs. 8–9). Structure: Abdominal segment VIII greatly reduced, mostly membranous; tergite consisting only of a short, medial, ligulate sclerite; pleurites and sternite undifferentiated. Epandrium simple, emarginate postero-medially. Xth lobes well developed, prominent, slightly divergent; interlobular depression deep, V-shaped; individual lobe quadrate, apex trilobate: outer sublobe acutely rounded, middle subsublobe small, central, angled inwardly, inner sublobe obtusely angled; inner margin straight, extending medially and directly to base of opposite margin; distal margin of lobe between outer and middle lobes slightly concave; inner arm poorly sclerotized, elongate, apex lobate, disjunct from same member opposite. Fused gonocoxites and hypandrium well sclerotized, forming capsule about as wide as long; posterolateral corners of gonocoxite strongly produced. Outer gonostylus moderately large (length about 0.7× midline length of hypandrium), an entire, subrectangular, lobe with concave inner margin. Inner gonostylus a narrow, porrect, smooth, simple, digitiform projection. Phallic complex straight, supinate, not recurved. Aedeagal filaments equal, with slightly flared apices, outer filaments strongly bowed near bases; lateral tine longer than rods, broad throughout, tapering slightly to complex apex; latter with dorsal hook on inner wall; canal wide toward the base and containing numerous long spiculae arising from inner wall and directed toward the apex; aperture subapical. Sperm pump and piston poorly developed, former without internal spines, latter with conspicuous, tubular, dorsal ejaculatory atrium attached to apodeme; apodeme a small, ventral, vertical flange. Subanal pouch wide, bowl-shaped; tegmen broad, apex trilobate, i.e., deeply incised on either side of strong, vertical, medial carina. Gonite large, broad, ovate; gonocoxal lobe poorly developed, posterior lobe elongate, anterior lobe expansive, ventral bridge complete beneath basiphallus. Sensilla: Epandrium with very numerous, short (toward anterior) to long (toward posterior) setiforms generally. Xth tergite lobe with medium setiforms generally and evenly spaced over central portion dorsally, longer toward apex; inner arm with few to several (5–8), small setiforms near the apex. Fused gonocoxites and hypandrium ventrally with numerous, medium setiforms generally spaced only over posterior half. Outer gonostylus with very numerous, medium setiforms generally and evenly spaced over outer surface and marginally, absent from middle of inner face. Epiproct with few (4–8) alveoliforms in dorsolateral group. Hypoproct with few (2) long setiforms apically.

Female (Fig. 7). Only a single, freshly emerged, alcohol-preserved specimen (allotype) available for coloration and measurements. Structural characters from pharate adults dissected from pupae. *Coloration*. Apparently as in male. *Size*. A medium-sized *Blepharicera*. Measurements (N = 1): Wing length 6.3. Leg segment lengths:

	foreleg	midleg	hindleg
femur	3.7	3.6	5.2
tibia	3.1	2.9	4.3
tarsus 1	1.4	1.4	1.9
2	0.67	0.66	0.64
3	0.42	0.41	0.38
4	0.30	0.29	0.32
5	0.44	0.43	0.38

Head (Fig. 7). Structure: Normal type, subholoptic. Suprafrons narrow, with a long, strongly convex carina. Clypeus elongate L/W = 2.3. Eyes approximate dorsally, interocular distance equal to combined diameters of 1–2 upper ommatidia; upper division well differentiated from lower (callis oculi very broad, anterior portion strongly striate), approximately equal to lower in area, somewhat flattened dorsally, 17 rows of ommatidia along mid-meridian; upper ommatidia larger (2.5×) than lower in diameter. Parietal sclerite broad, trapezoidal in outline. Proboscis short, free portion about 0.4× head width; mandibles present and complete; palpus 5-segmented, distal 4 palpal segment proportions 1.0–1.0–1.0–3.4. Antenna 15-segmented, flagellar segments narrowly elongate throughout, ultimate longer (1.8×) than penultimate, apical 3 segment proportions 1.0–0.9–1.7. Sensilla: Setiform groups on head capsule as follows: clypeals numerous to very numerous (26–45), general basally, more numerous and longer along distolateral margins. Seta over antennal socket. Parietal setae numerous to very numerous (18–38). Postocellars few (3–5), small, lateral. Medioccipitals absent. Supracervicals numerous (20), tiny. Occipitals separated from and larger than postgenals, numerous (32), long, uppers longer and heavier than lowers. Postgenals numerous (28–30), smaller toward center of group.

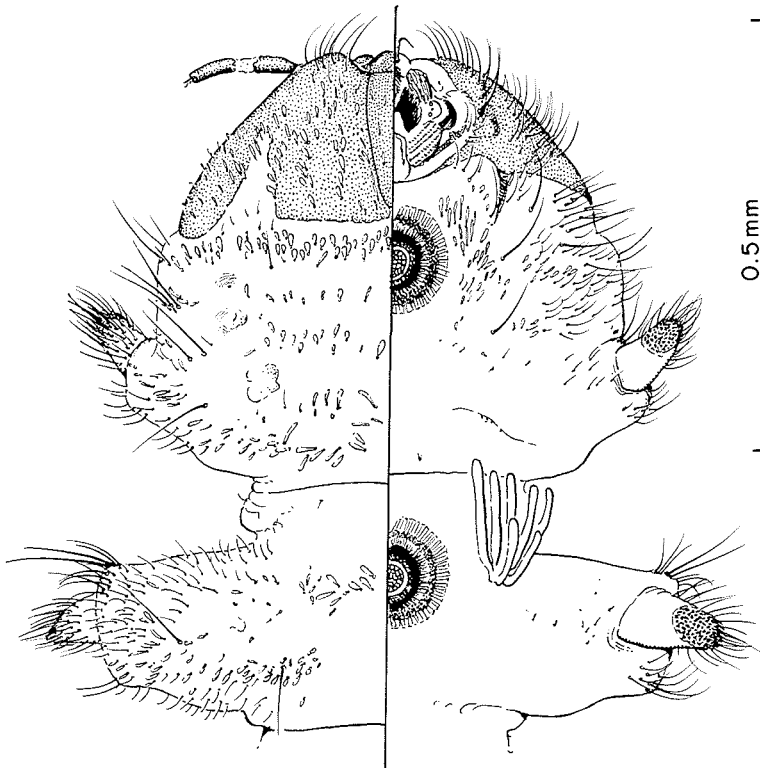
Thorax and appendages. Structure: Wing venation as in male. Tibial spurs 0–0–2 (inner twice length of outer). Hind basitarsus short. Progressive leg segment proportions: foreleg 0.8–0.5–0.5–0.6–0.7–1.5; midleg 0.8–0.5–0.5–0.6–0.7–1.5; hindleg 0.8–0.4–0.3–0.6–0.8–1.2. Sensilla: Macrotrichia of wing veins and setiform groups on thoracic sclerites as in male.

Terminalia. Structure: Posterior margin of VIIIth sternite lobe broadly bilobate, medial depression shallow; sclerotization in base of latter rectangular (much wider than long). Hypogynial plate subhexagonal, base slightly wider than apex; with weak transverse creases across base; apex acutely rounded (outer angle far from level of tip). Accessory gland elongate, decidedly dilated anteriorly. Spermathecae 3 in number, equal in size and shape, ovoid; necks very short to absent; ducts completely unsclerotized. Sensilla: Medial group of VIIth sternite with few (3) or numerous (12–18) small setae; posterior lobe with few to numerous (2–12), medium-sized

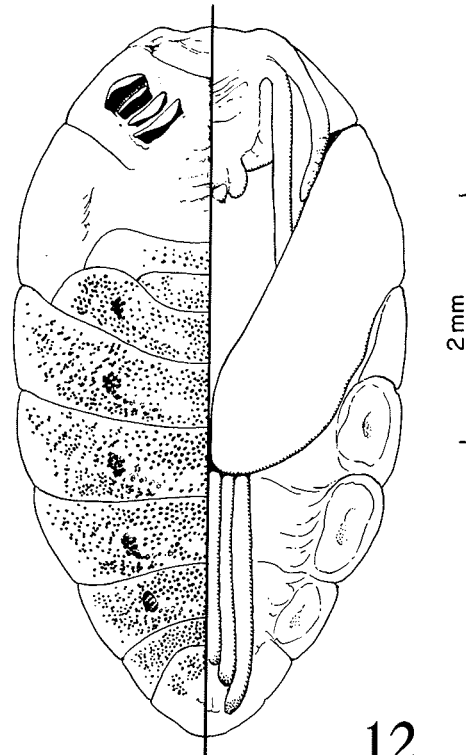
setae restricted to outer one-third. Short, stout apicodorsal setae of hypogynial lobe usually numerous (12–19). Epiproct with 1–2 apical setae. Alveoliforms of hypoproct few (3–6).

Pupa (Figs. 18, 22). *Integument*. Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral one-third), scutellar, and abdominal tergites densely papillose. Individual papillae finely spiculate, rounded, oval convexities. Pattern on abdominal tergites disperse, papillae more or less evenly spaced, slightly more dense toward the middle of sclerites, absent laterally. Cuticular structure between papillae irregular, thin and grooved areas (corresponding to pigmentary pattern as described below). *Coloration*. Surface reflection shiny; dark pigmentation broken by numerous, very fine, close-set, longitudinal, narrowly wavy, transparent furrows or lines and short, transverse “hyphens” between, the former appearing macroscopically as strong striae. *Size*. Medium. Measurements, male (N = 27): body length 4.5 (3.8–5.0), width 2.5 (1.9–2.8); female (N = 27): body length 5.2 (4.7–5.7), width 2.8 (2.5–3.1); male about 0.8× size of female. *Structure*. Outline shape elongate, L/W male = 1.8, female = 1.9; cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments convex, of II and III slightly wider than thorax, of IV often projecting slightly. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost coterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two plates slightly smaller and thinner than outers, slightly spreading; individual plates angularly seculate in outline.

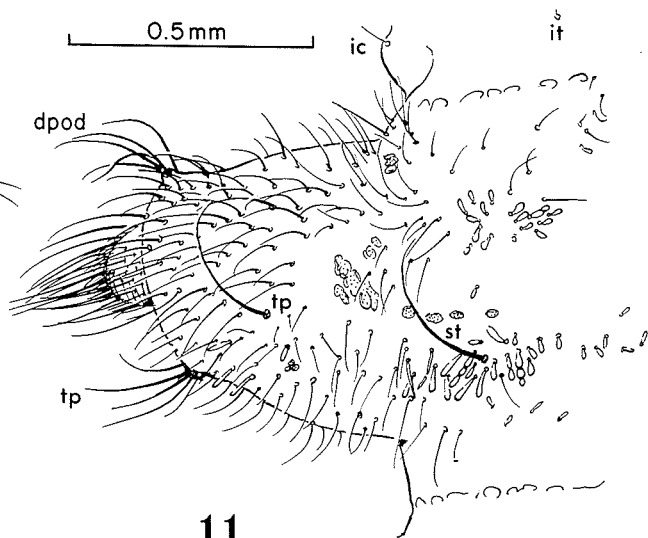
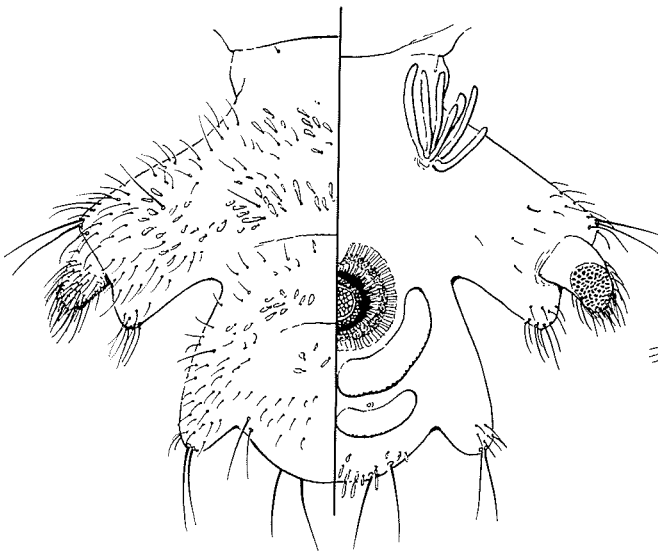
Larva (Fig. 14). Similar to *tenuipes*. *Integument*. Dorsally with distinct, but fine, mostly linear, corrugations, these absent ventrally. *Coloration*. Trunk evenly pigmented, medium brown, sclerotized portions dark brown to black. *Size*. Medium for the group. Measurements (N = 4): Body length (N = 3), 5.4 (5.3–5.6), antennal segment lengths, basal 0.16 (0.13–0.17), apical 0.19 (0.18–0.20). *General shape*. Cylindrical. *Head*. Antenna short, 2-segmented, intersegmental membrane wide; segment proportions 1.0–1.2. *Trunk*. Structure: Anterior division spheroid. Lateral margins of abdominal segments inclinous, truncate (pseudopods extending well beyond); dorsopseudopodal lobes small and poorly developed. Anal division trilobate: lateroterminal lobe acutely rounded; pleuron slightly convex, medioterminal lobe convex posteriorly, evenly rounded; terminal incision deep, V-shaped. Sensilla: Primary trunk sensilla: tP submedial, elongo-elliptoid, tM–T submedial, small, taeniaform, tI–VII submedial, lanciform, obscured by multiplication. stP lateromedial, taeniaform to setiform, stM–T lateromedial, elongo-elliptoid, stI lateromedial, acutiform, stII–VII lateromedial, setiform. Inner tpP far-lateromedial, disjunct from stP, seti-



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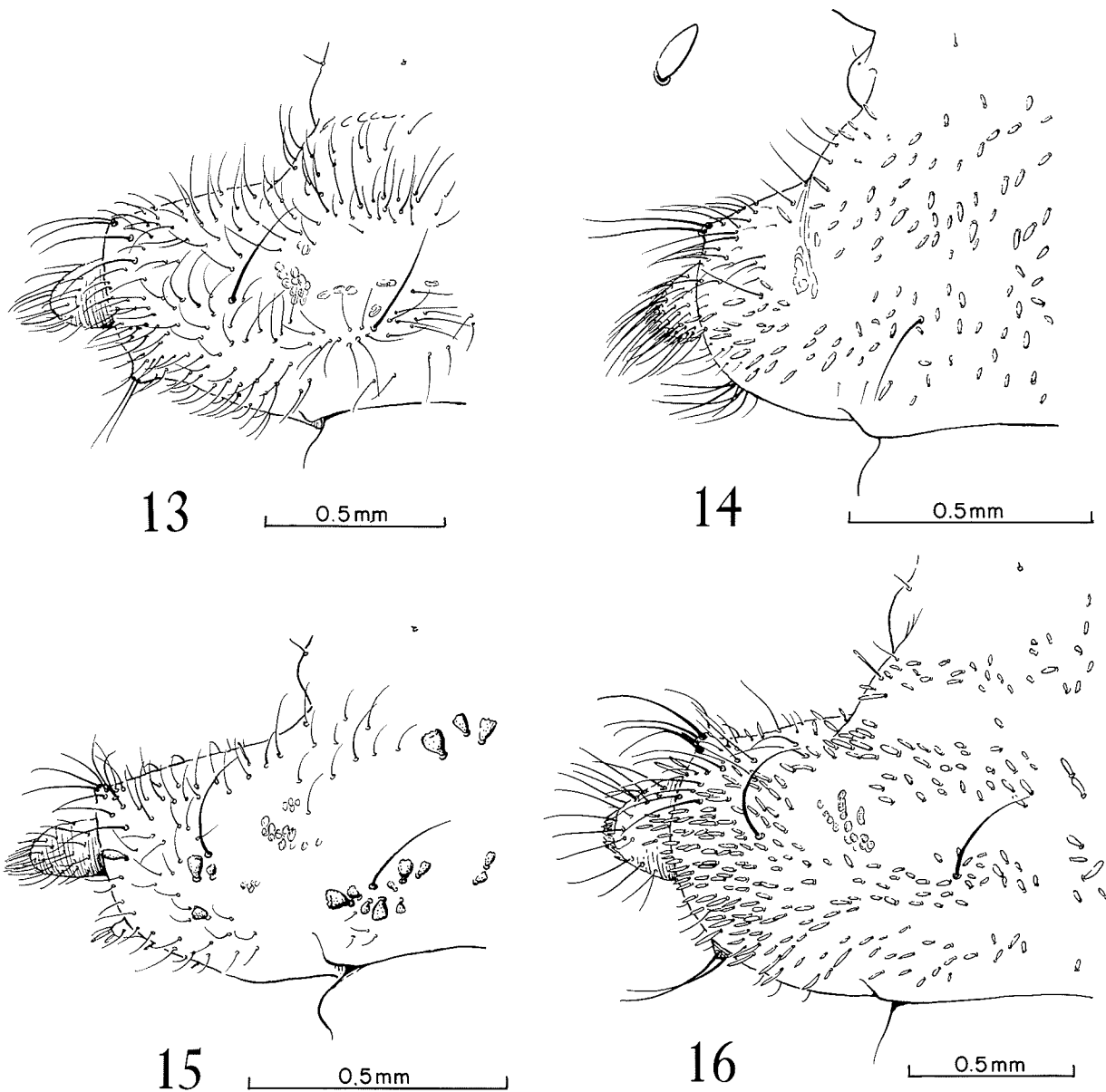


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Figures 10–12. *B. tenuipes*. 10. Larva (dorsum left, venter right). 11. Detail of dorsum of second abdominal segment of larva. 12. Pupa (dorsum left, venter right).



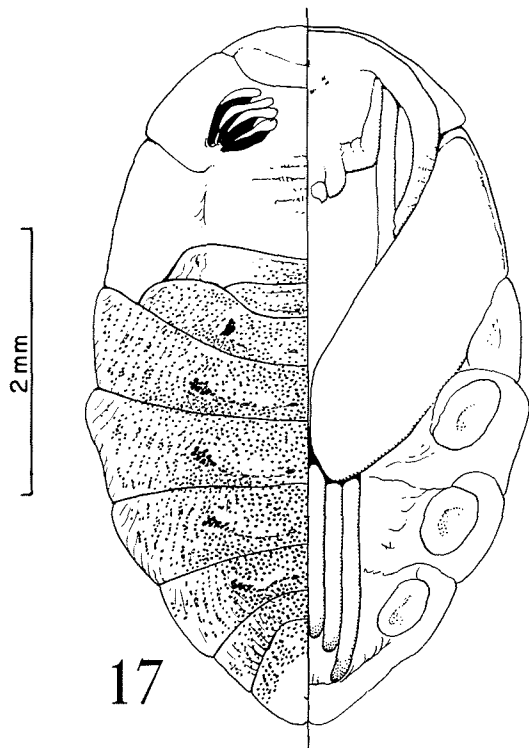
Figures 13-16. Larvae, left dorsal aspects of abdominal segments II. 13. *B. appalachiae*. 14. *B. coweetae*. 15. *B. similans*. 16. *B. williamsae*.

form, inner tpI-VII far-mediolateral, disjunct from and anterior to stI-VII, setiform. Outer tpI-VII near and slightly posterior to inner tp, lanciform to elongo-elliptoid. pdpodI-VII indiscernible. Inner and outer dpodM-T proximate, those of M sublateral, of T mediolateral, setiform, dpodI-VII on minute, anterolateral tubercle (= dorsopseudopodal lobe), setiform, inner and outer dpodVIII contiguous, at apex of lateroterminal lobe, setiform. ssP slightly lateral to ssM-T, decidedly larger than latter. Dorsal secondary trunk sensilla: numerous, more or less disperse but tending to be in two broad, transverse series medially, these merging laterally. Almost all elongo-elliptoid to elongo-claviform or lanciform,

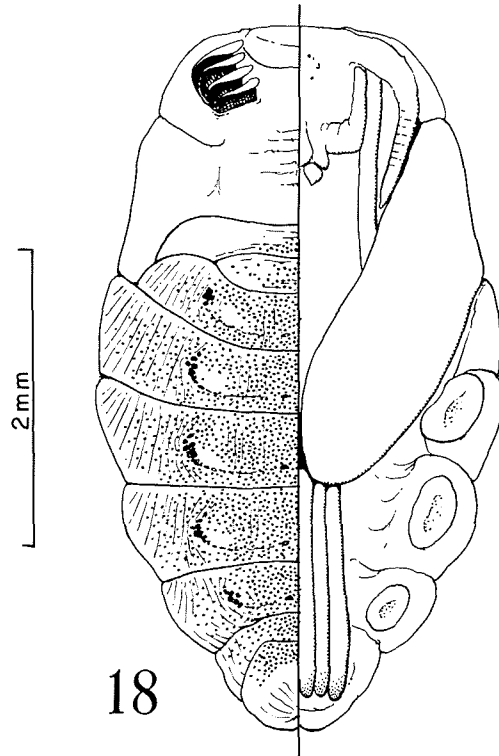
these short medially, becoming fairly long laterally; a few long setiforms intermingled laterally. Terminal setae 3-3, marginal.

SPECIMENS EXAMINED. Types. HOLOTYPE male (emerged from pupa), in alcohol with pupal skin (terminalia not dissected): NORTH CAROLINA, *Macon County*. Coweeta Hydrologic Laboratory, Lower Shope Fork, T. Georgian. Individually reared: collected 7 April 1984 as mature larva; pupated 13 April; emerged 5 May 1984 (LACM).

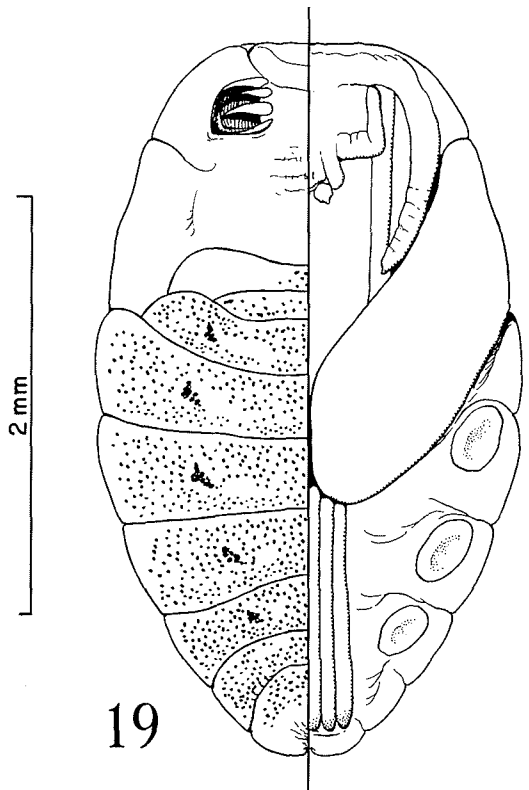
ALLOTYPE female (emerged from pupa), in alcohol with pupal skin (terminalia dissected and mounted on slide CLH 84-71). GEORGIA, *Rabun County*. Betty's Creek, T. Geor-



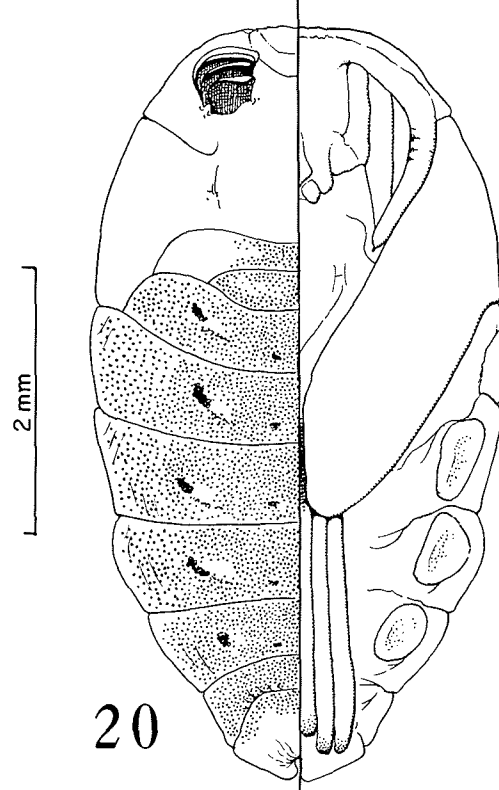
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Figures 17-20. Pupae, dorsal/ventral aspects. 17. *B. appalachiae*. 18. *B. coweetae*. 19. *B. similans*. 20. *B. williamsae*.

gian. Individually reared: collected 7 April 1984 as mature larva; pupated 16 April 1984; emerged 12 May 1984 (LACM).

Ten PARATYPE males, 5 PARATYPE females (extracted from pupal skins), variously dissected and mounted on slides no. CLH (males) 81-8, 84-1, 84-2, 84-39, 84-43, 84-44, 84-45, 84-46, 84-83a-d, 84-84a-d, (females) 84-47, 84-48, 84-49, 84-50, and 84-51. Same locality as holotype, 9 May 1981, T. Georgian (LACM, UGAM, USNM).

Additional specimens. NORTH CAROLINA, *Macon County*. Coweeta Hydrologic Laboratory, Lower Shope Fork, 2300 ft., 9 May 1981 (66 pupae); 24 April 1982 (9 larvae, 15 pupae). Dryman's Fork, 2100 ft., 21 April 1980 (26 pupae).

ETYMOLOGY. This species is named for Coweeta Creek in whose tributaries it was first found. "Coweeta" is treated as a noun in the genitive case. It is a Cherokee word associated with a major tribal settlement in the area, near Franklin, North Carolina. It has more recently been used by the U.S. Forest Service for its Coweeta Hydrologic Laboratory, also the type locality of the insect.

DISTRIBUTION. *B. coweetae* is known to date only from a roughly circular area about 17 km in diameter in the southern Appalachians, including the type locality and two other streams (Dryman's Fork, Macon County, North Carolina and Betty's Creek, Rabun County, Georgia), all within the Little Tennessee River drainage (Fig. 26).

ECOLOGICAL NOTES. The species is uncommon at the known sites of occurrence and little is known concerning its biology (See Ecological Notes under *B. appalachiae*).

LARVAE AND PUPAE OF OTHER SPECIES

Detailed descriptions of the larvae of the other species are being published by Hogue (in press). The following will verify the provisional identifications made by Hogue (1978), to which reference can be made for brief descriptions and illustrations. Minimal diagnostic features only are repeated here for clarification (see also the keys above). Diagnostic features consist primarily of the shape and distribution of the modified dorsal sensilla. The pupae are described in full and figured.

The immatures of *B. cherokea*, *diminutiva*, and *capitata* are still unknown.

Blepharicera similans Johannsen, 1929

Figures 15, 19, 23

Larva "B," Hogue, 1978:27, fig. 33.

The dorsal modified sensilla are large, of various sizes, dentate and basically short capitate to almost spherical in shape. They are arranged generally in two transverse rows, a longer series between the large subtergal setiform sensilla and a

shorter anteromedial row; a few also are associated with the large, inner, tergopleural setiform sensilla.

Pupa (Figs. 19, 23). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, without papillae. Metascutal (medially only), scutellar, and abdominal tergites moderately densely papillate. Individual papillae smooth, rounded, oval convexities. Pattern on abdominal tergites disperse, papillae more or less evenly spaced, slightly more dense medially, absent far laterally. Cuticle between papillae uniform in structure. *Coloration.* Surface reflection shiny; pigmentation even. *Size.* Medium. Measurements (northern material, specimens from North Carolina, Shope Creek distinctly smaller, 0.7), male (N = 10): body length 4.1 (3.8-4.5), width 2.4 (2.2-2.8); female (N = 10): body length 5.0 (4.4-5.3), width 2.9 (2.5-3.3); male about 0.7 × size of female. *Structure.* Outline shape almost ovoid, L/W male = 1.4, female = 1.4. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments symmetrically convex, those of II and III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3 × length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, midleg less, hindleg less than either; mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular secutate in outline.

Blepharicera tenuipes (Walker, 1848)

Figures 10-12, 24

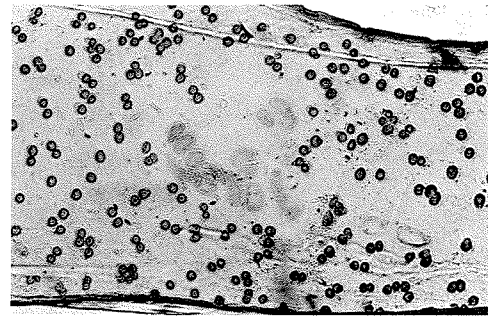
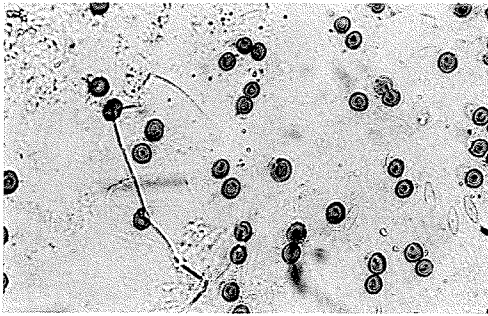
Larva "A" Hogue, 1978:27, fig. 30.

The dorsal modified sensilla are short, elongo-claviform. They are arranged in two irregular transverse rows, a longer posteromedial series including the subtergal sensilla, and a shorter anteromedial row. Laterally the sensilla are mostly setiform (Figs. 10-11).

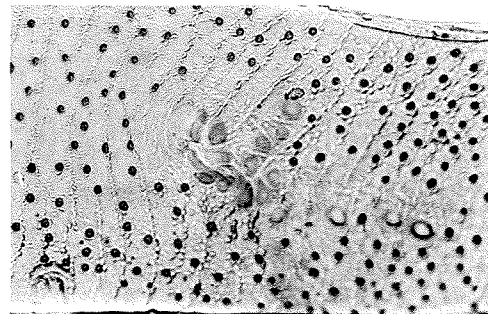
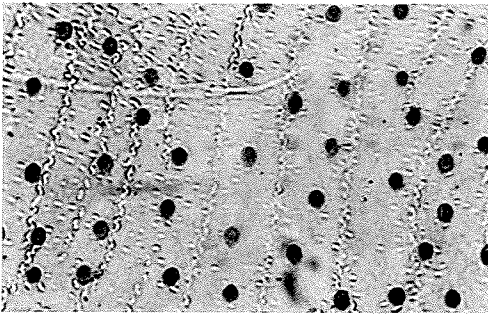
Pupa (Figs. 12, 24). *Integument.* Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral one-third), scutellar, and abdominal tergites moderately densely papillate. Individual papillae smooth, rounded, oval convexities. Pattern disperse, unevenly spaced, papillae often arranged in pairs but not in fused diads, mainly in areas of abdominal tergites lateral to muscle scars, more or less evenly spaced in medial area between scars; slightly more dense medially, absent laterally.

→
Figures 21-25. Pupae, *Blepharicera tenuipes* group. Photomicrographs of tergites of abdominal segment II, showing arrangements of integumentary papillae. Dorsomedial third of sclerite at right, detail of area lateral to major muscle scar at left. 21. *B. appalachiae*. 22. *B. coweetae*. 23. *B. similans*. 24. *B. tenuipes*. 25. *B. williamsae*.

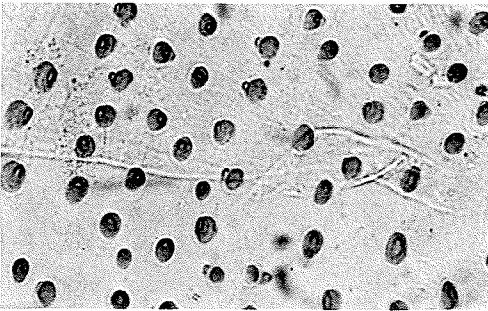
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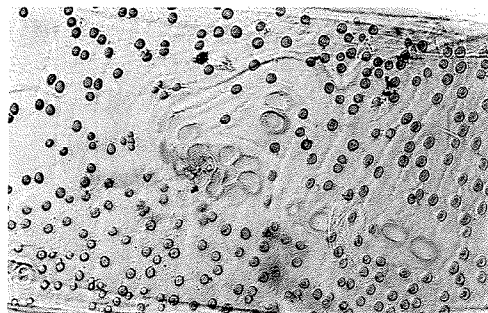
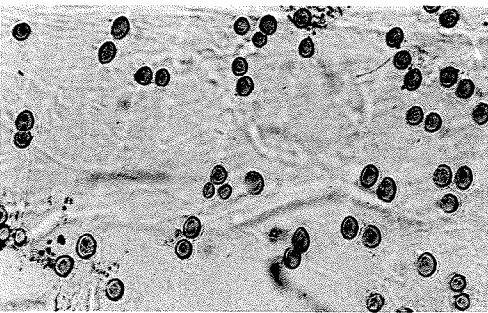
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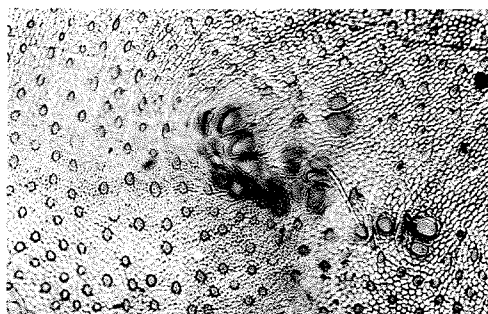
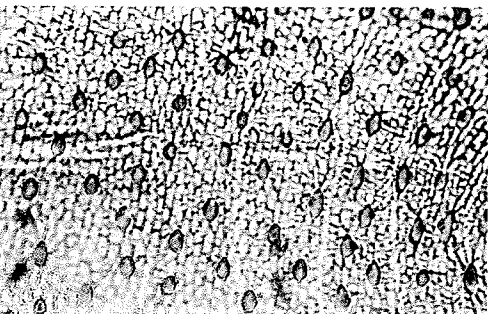
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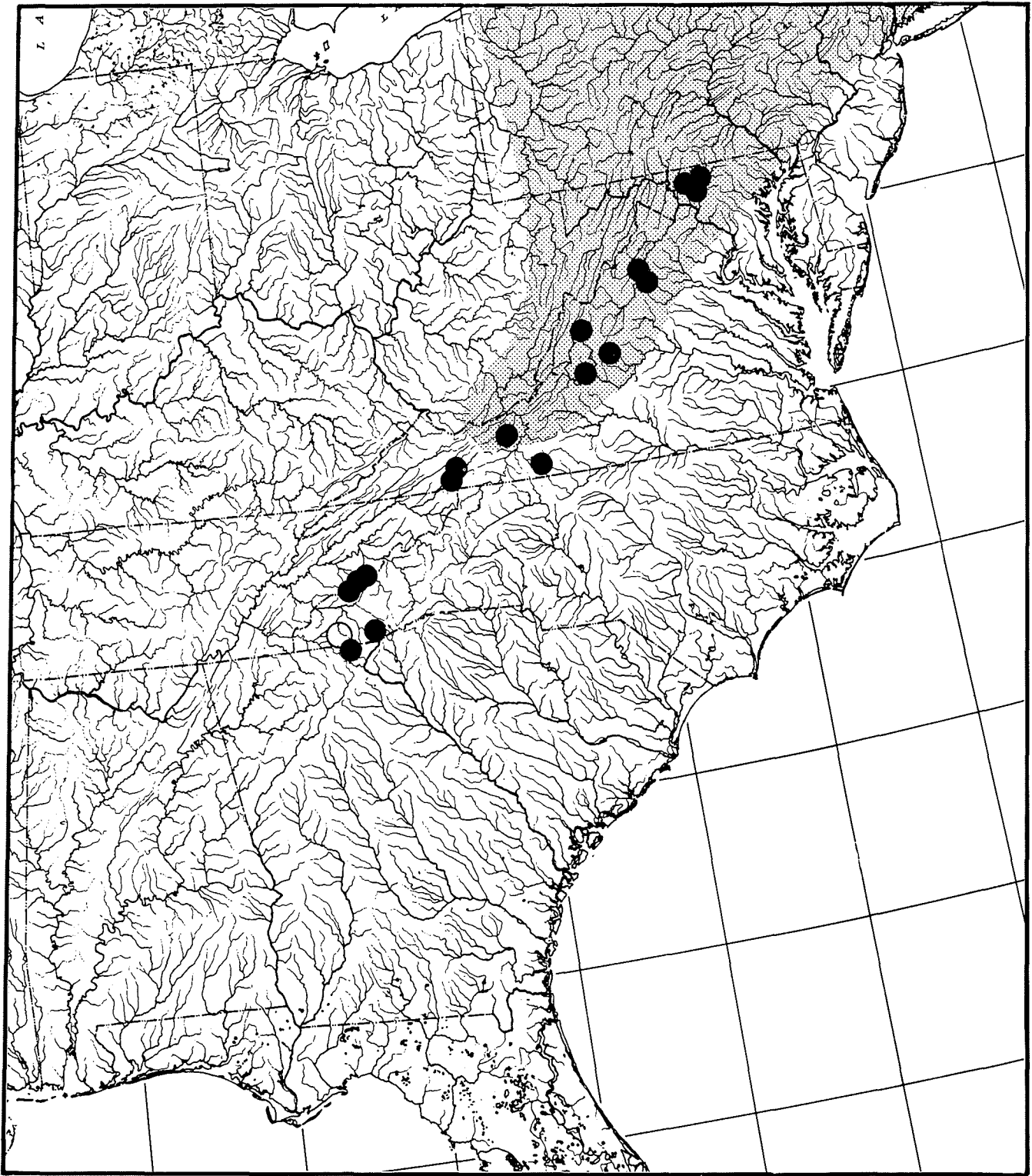


Figure 26. Drainage systems of eastern United States and Canada showing distribution of the *Blepharicera appalachiae* (solid circles) and *coweetae* (open circle). Shaded area represents range of *Blepharicera tenuipes*. Location of Coweeta Hydrologic Laboratory area indicated by open circle.

Cuticle between papillae uniform in structure. *Coloration*. Surface reflection shiny; pigmentation even. *Size*. Medium. Measurements, male (N = 12): body length 4.6 (4.1–4.9), width 2.5 (2.3–2.8); female (N = 14): body length 5.5 (5.3–5.8), width 3.2 (3.0–3.5); male about 0.6× size of female. *Structure*. Outline shape almost ovoid, L/W male = 1.8, female = 1.8. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments symmetrically convex, of II and III slightly wider than thorax, equally projecting all around. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost coterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seculate in outline.

Blepharicera williamsae Alexander, 1953

Figures 20, 25

Larva "D" Hogue, 1978:29, fig. 31.

The larva of this species is extraordinarily large for the *B. tenuipes* group (mean body length 8.6 mm, range extremes 7.2–10.5 mm). The integument is also pigmented unevenly, i.e., dark dorsomedially, light cream laterally, presenting a longitudinally striped appearance. The dorsal modified sensilla are short, oviform, ellipsoid or pyriform and more or less densely distributed evenly over the entire dorsal surface (slightly more dense laterally) (Fig. 16).

Pupa (Figs. 20, 25). *Integument*. Dorsum well sclerotized. Pleural margins not sclerotized ventrally. Frontal, scutal, branchial, and alar sclerites smooth, completely without papillae. Metascutal (except lateral half), scutellar, and abdominal tergites densely papillose. Individual papillae finely spiculate, small, rounded, oval convexities; pattern on abdominal tergites general, papillae more or less evenly but closely spaced, slightly more dense medially, absent marginally. Cuticle between papillae finely reticulate. *Coloration*. Surface reflection dull; pigmentation irrorate, in concordance with reticulate structure. *Size*. Medium. Measurements, male (N = 10): body length 5.5 (5.1–5.9), width 3.1 (2.8–3.4); female (N = 10): body length 6.7 (6.1–7.5), width 3.7 (3.4–4.1); male about 0.8× size of female. *Structure*. Outline shape almost ovoid, L/W male = 1.8, female = 1.8. Cross section convex, sides declivous all around. Dorsal sclerites: lateral margins of abdominal segments asymmetrically convex, of II and III slightly wider than thorax, of IV projecting slightly. Branchial sclerite smoothly curving. Ventral sclerites: antennal case extending well beyond base of wing case in both sexes (about 0.3× length), apex straight. Apices of leg cases in male coterminate; in female tip of hindleg most extended, foreleg and midleg much less, these almost coterminate. Mandibular case small in male, much longer and fuller in female. Branchiae: medium, erect, approximate, parallel, projecting forward just

short of plane of anterior margin. Plates of each branchia lobate, rigid, parallel, inner two slightly smaller and thinner than outers, slightly spreading; individual plates angular seculate in outline.

Larva F Hogue, 1978

Larva "F" Hogue, 1978:30, figs. 34, 36.

The existence of very distinctive larvae with gross, dorsal, conical protuberances in the center of the abdominal segments with which no equally distinct adults can be associated is a puzzling phenomenon. Such larvae appear among normal larvae of other species in the *tenuipes* group (*tenuipes*, *appalachiae*), suggesting that they are variants expressing a developmental anomaly. This is the conclusion of Zwick (pers. comm.), who also finds the same condition among larvae of European *Blepharicera* and species of *Liponeura*. There is a tendency in some larval individuals and even populations for a centripetal crowding and multiplication of secondary sensilla on the disc of abdominal segments, indicating hyperactive epidermal cell growth in the region which might be expressed maximally by hypertrophy of the entire integument. Larva F, therefore, should not be considered a distinct species until more knowledge can be acquired regarding the morphological significance of this type of larva.

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Dr. Wayne Swank kindly provided access to streams at the U.S. Forest Service's Coweeta Hydrologic Laboratory. Equipment for rearings was made available by Dr. J.B. Wallace of the Department of Entomology, University of Georgia. A. Huryn and J. O'Hop gave invaluable assistance in the field.

For the use of material we wish to acknowledge the following repositories and institutions, including our own (listed alphabetically by the abbreviation cited under Specimens Examined for each of the species), and thank their respective curators who kindly arranged loans and provided information:

- BCK personal collection, Boris Kondratieff, New Ellenton, South Carolina.
- BYU Bean Life Science Museum, Brigham Young University, Richard W. Baumann.
- CNC Canadian National Collection, B.V. Peterson.
- CU Cornell University, L.L. Pechuman.
- LACM Natural History Museum of Los Angeles County.
- UGAM University of Georgia Entomological Museum.
- OSU Ohio State University, Paul H. Freytag.
- ROM Royal Ontario Museum, Glenn B. Wiggins.
- USNM U.S. National Museum of Natural History, Alan Stone.

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