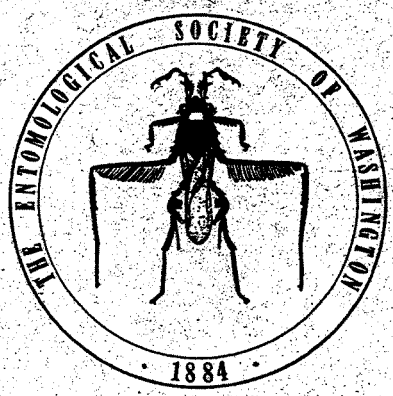
REVISION OF THE NET-WINGED MIDGES OF THE GENUS BLEPHARICERA MACQUART (DIPTERA: BLEPHARICERIDAE) OF EASTERN NORTH AMERICA



BY

GREGORY W. COURTNEY

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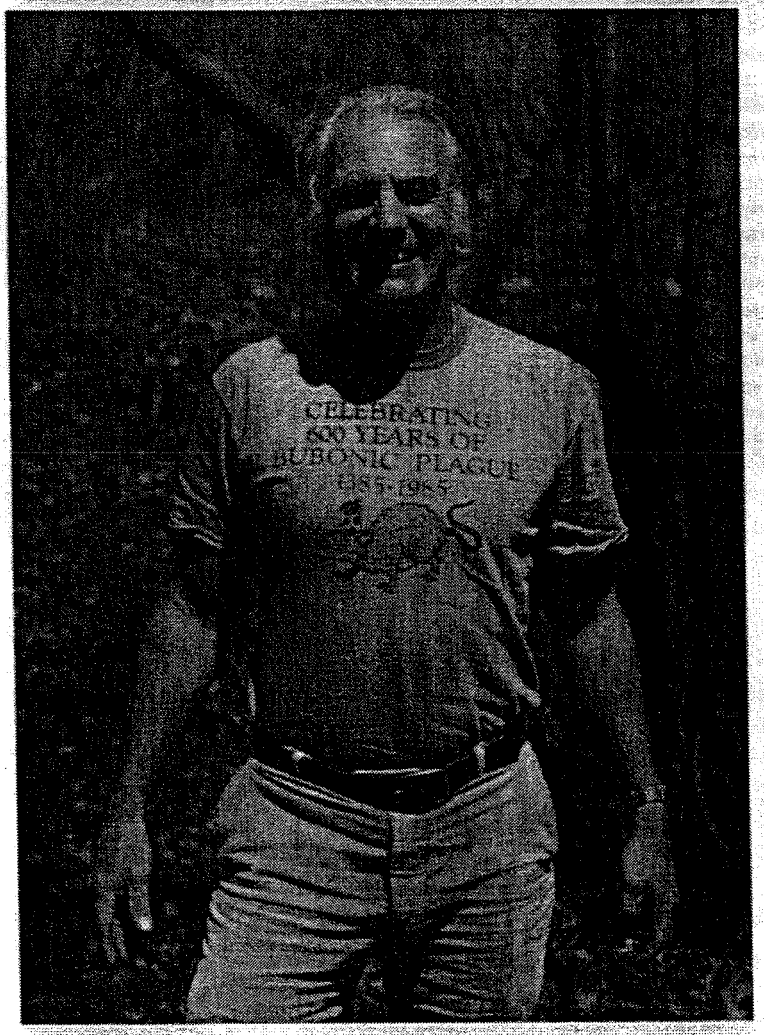
Dedicated to

Charles L. Hogue (1935–1992),
naturalist, student of torrenticolous flies, and friend



Charlie Hogue at Logan Canyon, Utah, 1985
(photo by J.N. Hogue)

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Abstract.—The net-winged midges (Diptera: Blephariceridae: *Blepharicera* Macquart) of eastern North America are revised to include 16 species. Seven new species are described: ***B. caudata*, n. sp., *B. chattooga*, n. sp., *B. corniculata*, n. sp., *B. magna*, n. sp.,** and ***B. tuberosa*, n. sp.** from the southern Appalachians; ***B. gelida*, n. sp.** from the central and southern Appalachians; and ***B. hispida*, n. sp.** from the central and northern Appalachians. Previously unknown life stages of *B. capitata* Loew, *B. cherokea* Hogue, *B. diminutiva* Hogue, and *B. separata* Alexander, a species raised from synonymy, are described, and a redescription of adult *B. separata* is given. Also provided are an overview of blepharicerid natural history, keys to larvae, pupae, and adults of all eastern *Blepharicera*, and brief discussions of the bionomics and distribution of each species.

Key Words: Blephariceridae, net-winged midges, *Blepharicera*, Appalachians

INTRODUCTION

Net-winged midges (Diptera: Blephariceridae) are one of the most distinctive and specialized insect families. The group contains approximately 300 described species, with representatives on all major continents (except Antarctica) and several continental islands (e.g., Madagascar, New Zealand, Sri Lanka). The immature stages of most species inhabit rapidly flowing, or torrenticolous, streams. Larvae show many adaptations to current-exposed habitats, including a cephalothorax (fused head, thorax and first abdominal segment) and six ventral suctorial discs. Larvae are grazers, using specialized mouthparts to feed primarily on epilithic algae on current-exposed rocks. Pupae are equally well adapted to torrential streams, being dorsoventrally compressed, streamlined, and attached immovably to rocks. Adult blephariceridsare slender-bodied, long-legged, and show a diversity of habits. Additional details about blephariceridnatural history are provided later.

Blepharicera Macquart is one of the most widespread blephariceridgenera worldwide and, within the Nearctic Region, is the only net-winged midge found in both western and eastern North America. Eastern North America contains two of the earliest described blephariceridspecies, *B. tenuipes* (Walker 1848) and *B. capitata* (Loew 1863). These and most early studies of eastern *Blepharicera* (e.g., Kellogg 1900b, 1907; Johannsen 1929; Alexander 1953) dealt primarily with isolated species descriptions, taxonomic notes, or ecological observations. More recent taxonomic investigations of the fauna are limited to two papers (Hogue 1978, Hogue and Georgian 1986). All blephariceridsfrom eastern North America belong to the *Blepharicera tenuipes* group, a presumably monophyletic assemblage containing 16 species: *B. appalachiae* Hogue and Georgian, *B. capitata* Loew, *B. cherokea* Hogue, *B. coweetae* Hogue and Georgian, *B. diminutiva* Hogue, *B. separata* Alexander, *B. similans* Johannsen, *B. tenuipes* (Walker), *B. williamsae* Alexander and the seven new species described in this paper.

Hogue (1987) provided detailed information on adult character systems, particularly male genitalia, but the lack of character data for other life stages has hindered construction of complete and effective keys. Structural homogeneity of larvae is typical of *Blepharicera,* in which larvae of some species are often separable only by subtle differences in chaetotaxy or cranial color. Identification of early-instar larvae is even more difficult. Larvae and pupae are encountered most often in faunal surveys and ecological studies and, consequently, are the life stages for which keys are needed most. In this respect the Nearctic fauna, particularly the *B. tenuipes* group, has been especially problematic, mostly because the group contains several new species and many others (*B. capitata, B. cherokea, B. diminutiva, B. separata*) for which immature stages are undescribed. This paper provides general information about blephariceridnatural history, descriptions of new Appalachian species, descriptions of previously unknown life stages of described species, and diagnoses and a general review of the distribution and bionomics for all eastern species. Keys to mature larvae, pupae, males and females of all Appalachian species are included. This paper is part of a broader investigation of the systematics, cytogenetics, and life histories of Nearctic *Blepharicera.*

METHODS

Material.—This study is based on examination of larvae, pupae, and adults of all known species of Nearctic *Blepharicera.* Most specimens were taken during 1990–1999 by aerial collections or standard benthic sampling, including rock-wash methods (Courtney 1991b). Association of larvae and pupae was based partly on the ontogenetic method (Hogue 1989), which involves dissection of the pharate individual from the earlier stage. Definitive association

of pupae and adults was accomplished through this method and by individual rearings of pupae attached to rocks (Courtney 1998). Additional specimens were borrowed from, or are deposited with, the following institutions (acronyms used throughout the text): BMNH, The Natural History Museum, London, England; CNC, Canadian National Insect Collection, Ottawa, Canada; CUI, Cornell University, Ithaca, New York; CUAC, Clemson University Arthropod Collection, Clemson, South Carolina; FAMU, Florida A&M University, Tallahassee, Florida; GSMNP, collection of the Great Smoky Mountains National Park, Gatlinburg, Tennessee; ISU, Iowa State Insect Collection, Ames, Iowa; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NCDWQ, North Carolina Division of Water Quality, Raleigh, North Carolina; PUWL, Purdue University Insect Collection, West Lafayette, Indiana; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Specimen preparation.—Field-collected and reared adults were fixed primarily in 70–80% EtOH, whereas larvae and pupae usually were placed in 95% EtOH or Carnoy's solution (one part acetic acid: three parts 98% ethanol). Morphological studies were based on whole-animal preparations, slide mounts, and scanning electron microscopy (SEM). Most slide-mounted material was cleared in cedarwood oil and mounted in Canada balsam, following procedures described elsewhere (Courtney 1990a). Additional material was prepared by removing soft tissues with dilute (approximately 10%) potassium hydroxide (KOH). Specimens treated in KOH were either mounted permanently in Euparal or converted to temporary slide mounts in glycerin. Many adult specimens were dissected (genitalia removed, cleared in KOH, stored in glycerin microvials) then dried either chemically with hexamethyldisilazane (HMDS) or by using a critical point dryer. Specimens were examined using an Olympus SZX-12 dissecting microscope and a Nikon E-800 compound microscope, and drawings were rendered with the aid of drawing tubes on both systems. Photomicrography was accomplished with a H-III Microflex camera, using color print or slide film. Drawings and light micrographs were scanned with a UMAX Powerlook II. Material for SEM examination was sonicated briefly (5–10 s) in EtOH or an EtOH-KOH mixture and prepared by critical point drying and gold- or gold-palladium coating in a sputter coater. Material was examined with either a Cambridge Stereoscan 250 or JEOL JSM-5800LV. The latter SEM captured direct digital images, whereas the Cambridge recorded standard photographic images on Tri-X Pan Professional or Plus-X film; the latter were then scanned.

Terms for structures.—Terms for structures come primarily from my own studies of blephariceromorph flies (Courtney 1990a, 1991a, 1994), investigations of Blephariceridae (Stuckenberg 1958; Alexander 1963; Zwick 1977, 1990; Hogue 1978, 1981, 1987; Hogue and Bedoya-Ortiz 1989; Hogue and Georgian 1986; Courtney 2000), or reviews of Diptera (Hennig 1973; McAlpine 1981; Teskey 1981; Wood and Borkent 1989; Courtney et al. 2000). Terms for larval and adult cranial chaetotaxy are from Hogue (1978), and terms for male terminalia are based primarily on Sinclair (2000), as summarized by Courtney (2000). Interpretations that vary from previous blepharicerid work include (1) gonocoxal lobe (= inner dististyle of Alexander, Stuckenberg, and Zwick, inner gonostylus of Hogue); (2) ventral paramere (= parameres of Zwick, lateral tines of Hogue); (3) dorsal paramere (= tegmen of Stuckenberg and Zwick, ventral plate of Hogue); (4) lateral parameral lobes (= gonites of Hogue). Descriptions of larval structures are based mostly on fourth instars, because of their size, relative development of structures, and the difficulty in identifying early-instar lar-

vae. Homologies were determined primarily by general resemblance of structure, spatial relationships, landmark features (e.g., primary sensilla), and post-hatch ontogenetic data (e.g., histoblast location).

Descriptive format.—Diagnoses are provided for all species. Complete descriptions of adults, pupae, and mature larvae are given for new species and for previously unknown life stages of described species; otherwise, I refer to the original description or the most recent review (Hogue 1987). When applicable, sample sizes are indicated prior to each data set, with values presented as a mean followed in parentheses by a range. Larval "cranial width" refers to the distance between antennal bases. Adult palpomere proportions represent the length of proximal to distal articles. Leg segments were measured along the dorsal margin; segment percentages are mean values for segment length: total leg length. Abbreviations for label and locality data include the following: Bk = Brook; Br = Branch; CG = Campground; ca = approximately; CHL = Coweeta Hydrological Laboratory; Ck = Creek; Co = County; confl = confluence; DWG = Delaware Water Gap; E = East; FS = (United States) Forest Service; Fk = Fork; GSMNP = Great Smoky Mountains National Park; Hwy = Highway; jct = junction; M = Middle; mi = mile(s); N = North; NF = National Forest; NP = National Park; nr = near; R = River; Rd = Road; Rt = Route; S = South; trib = tributary; W = West; Xing = crossing/bridge. Abbreviations for life stages are L = larvae; P = pupae; Pex = pupal exuviae; A = adult. Under discussions of bionomics, "season of activity" or "activity period" refers to the period when larvae and pupae are present.

Natural History

The larvae and pupae of blepharicerids are highly specialized for life in the cascades, rapids, and waterfalls of mountain streams. Although larvae generally inhabit submerged substrata, some species (e.g., *B. diminutiva*) prefer the madicolous- or hygropetric habitats of waterfall and stream margins. Blepharicerids have four larval instars, which can be separated by a variety of morphological features: presence/absence of eversible prolegs and an egg burster (Fig. 101), both of which are characteristic of first instars; cranial width; and number of gill filaments. Larval instars I-IV of *Blepharicera* possess, respectively, zero, one, three or four, and six or seven filaments per gill. All larval instars remain attached to rocks through the action of six ventral suctorial discs, which function as true hydraulic suckers. Details of their structure are provided elsewhere (e.g., Kellogg 1900b, Komárek 1914, Bischoff 1928, Rietschel 1961, Hermann et al. 1975, Courtney et. al. 2000). Suctorial discs function on smooth substrata such as water-polished rocks and even glass, but generally not on organic substrata and sedimentary or marl-covered rocks. The pattern of suctorial disc action and larval movement is complex, behavior dependent, and largely predictable (Frutiger 1998). Alarm or escape behavior involves rapid lateral movement, whereas routine locomotion (e.g., during feeding) is characterized by relatively slow forward progression. Larval blepharicerids often remain attached to rocks even when disturbed, which explains their general absence in kick- and drift samples. Larvae are grazers (scrapers), feeding on the thin film of algae, bacteria and other organic matter (= periphyton) on submerged rocks. Studies of Appalachian species suggest that diatoms are the major component of their diet (Georgian and Wallace 1983, Alverson 2000). Food particles are dislodged from the substratum by robust mandibles and swept toward the mouth by enlarged, complex maxillae (Figs. 99–100).

Prior to pupation, larvae often move to specific areas of the rock or stream, including depressions on the upper, downstream faces of rocks or (e.g., in *B. diminutiva*) the splash zones on emergent rocks. During pupation, initial eclosion is through ecdysial

lines between the larval genae and frontoclypeal apotome. The emerging pupa sheds the larval skin and simultaneously attaches itself to the rock by three pairs of ventrolateral adhesive discs. Newly emerged pupae are white with dark respiratory organs, but turn dark within a few minutes (Tonnoir 1930, Alexander 1963). In some Appalachian streams, individual rocks can harbor hundreds of pupae, most oriented in the same direction (Courtney 1998: fig. 1). Blepharicerid pupae are well adapted to life in high current velocities, being dorsoventrally compressed and streamlined. Although pupal shape is highly streamlined, pupae typically orient with their thick anterior end facing downstream (i.e., like a "bluff body"). Such an orientation promotes formation of a downstream vortex across the respiratory organs (Pommen and Craig 1995), which may enhance delivery of oxygen to the respiratory surfaces. The duration of the pupal stage varies with species and stream temperature, but typically lasts between 2–3 weeks.

Emergence requires that the pupa be attached firmly to the substratum. The emerging adult splits the pupal ecdysial lines by applying downward pressure against the substratum. Observations of laboratory-reared adults indicate that some individuals cannot simply crawl out of the pupal case, relying at least partly on the aid of current or an air bubble. Under field conditions, emergence can be quite brief, requiring from three to five minutes (Alexander 1963). Because the wings develop to full size within the pupal case and merely unfold during emergence, adults can fly immediately upon reaching the water surface. My own field and laboratory observations suggest that some species emerge mostly at night or during dawn or dusk, whereas other species emerge primarily during the day.

Adult blepharicerids show a diversity of habits. Females of most *Blepharicera* are insect predators, sucking the blood of mayflies, stoneflies, and other soft-bodied insects. The latter includes many other Diptera: e.g., Chironomidae, Dixidae, Tipulidae, and even smaller Blephariceridae. A feeding female typically holds the prey with its hindlegs, macerates the insect with the labrum, inflicts lacerations with the mandibles and hypopharynx, and siphons out the body fluids. The food of males and nonmandibulate females is unknown, but nectarivory is likely in many species. Adults of most species are short-lived (1–2 weeks), with the male lifespan somewhat less than that of the female. Although night-emerging species have been collected at lights and appear to be primarily nocturnal, most species are active during the day. Adults of most species rarely venture beyond the riparian zone, where they frequent the undersides of branches extending over the stream. Adults of many Appalachian *Blepharicera* frequent the undersides of leaves, where they rest with the wings held at a moderate angle to the body and the hindlegs extended in a knock-kneed fashion. Mating typically occurs shortly after emergence, sometimes even with the female still holding the pupal exuviae (Hogue 1981). Copulating individuals often are seen on vegetation or emergent rocks, and oviposition occurs soon afterwards. Small clusters of eggs are cemented to wetted rocks or beneath the water surface. In some species the female crawls beneath the water and oviposits on submerged rocks.

Phenological data for Nearctic blepharicerids are limited to a few detailed studies (e.g., Courtney 1991a, Johns 1996, Courtney, unpublished data), plus numerous anecdotal observations and collection records. These various sources of information suggest that most Appalachian *Blepharicera* are univoltine and exhibit "fast-seasonal" (Hynes 1970) or "heterodynamic" (Butler 1984) development, which is characterized by rapid growth after a long period of dormancy (e.g., late-summer and winter egg diapause in most *Blepharicera*). In contrast, some species (e.g., *B. similans*) appear to be multivoltine. In most species, post-diapause growth and development (i.e., egg

hatching) begins when stream temperatures increase during the spring. Other stimuli (e.g., photoperiod) could also be involved (Dudley et al. 1990). Development time (i.e., egg hatch to adult emergence) varies substantially among and sometimes within species, and depends largely on thermal regime. The larval activity period of winter species (e.g., *B. magna, B. coweetae, B. williamsae*) can be greatly protracted relative to those of spring or summer species. Asynchronous life histories are typical of these and many other species, with a long period of egg hatching presumably causing much of the asynchrony.

One of the striking features of the eastern Nearctic blepharicerid fauna is the relatively high level of sympatry. Larval blepharicerids constitute a guild of highly specialized grazers with seemingly narrow habitat requirements, yet sympatry among congeners is common and frequently includes co-occurrence of five or more species. Mechanisms of reproductive and ecological isolation can be complex, including differences in seasonality, macrohabitat, microhabitat, and adult-emergence times. Studies of western Nearctic blepharicerids (Courtney 1991a) have shown coexistence of up to five species of blepharicerids, with conspicuous and predictable patterns of spatiotemporal separation. Streams in eastern North America demonstrate even higher levels of sympatry, with coexistence of five or six species at many sites and even more (up to 10 species) in some streams in the southern Appalachians. Temporal separation, microhabitat partitioning, and differences in adult emergence times are among the possible isolation mechanisms (Johns 1996, Courtney, unpublished data). Larval dietary specialization could provide an additional mechanism for high levels of sympatry (Alverson 2000).

Although often considered rare, blepharicerids can be a significant component of stream ecosystems. In some western Nearctic streams, densities of immatures can exceed 1,000/m^2 at certain times of the year (Courtney, unpublished data), making blepharicerids not only a dominant grazer but one of the most abundant insects. Comparable densities can occur in Appalachian streams (Johns 1996, Courtney, unpublished data). Densities often translate into substantive invertebrate production (Anderson 1992). Perhaps because of their specialized and demanding habitat, the immature stages of blepharicerids are preyed on by relatively few organisms. Among the most important predators of pupae are larval rhyacophilid caddisflies, which leave distinctive holes in the pupal cuticle. Additional predators include perlid stoneflies, which are known to feed on *Blepharicera* larvae (Johns 1996). The significance of net-winged midges as fish food is underappreciated, yet blepharicerids can be an important food for trout in Appalachian streams (Courtney and Duffield 2000). Furthermore, because blepharicerids inhabit clean, cool, well-oxygenated streams, these flies are potentially useful bioindicators of water quality (Lenat 1993). Additional information about blepharicerid natural history is available from several general treatments of the family (Alexander 1963, Zwick 1977, Hogue 1981, Courtney 2000).

Blepharicera Macquart 1843

Blepharicera Macquart 1843: 61. Type species: *Blepharicera limbipennis* Macquart 1843: 63 (= *fasciata* (Westwood 1842)) [original designation]; Curran 1934: 62 [generic key]; Hogue 1987: 1 [review of Nearctic fauna]; Lenat 1993: 289 [as bioindicator].

Asthenia Westwood 1842: 94. Type species: *Asthenia fasciata* Westwood 1842: 94. [junior homonym of *Asthenia* Hübner 1825 and *Asthenia* Westwood 1841].

Blepharocera Macquart: Loew 1858: 107 [unjustified emendation of *Blepharicera*]; Loew 1869: 85 [review of family, adult keys], 1877: 56 [review of family, adult keys]; Osten Sacken 1895: 148 [review of family]; Kellogg 1903: 188 [review of Nearctic fauna]; Aldrich 1905: 171 [cat-

alog]; Curran 1923: 267 [generic key]; Johannsen 1934: 50 [review of immature stages, larval key]; Alexander 1953: 813 [review of family, generic key]; 1963: 39 [review of family, generic key].

Blepharoptera Macquart: Loew 1863: 298. [*lapsus calami* for *Blepharocera*].

Parablepharocera Kitakami 1931: 97. Type species: *Blepharicera shirakii* Alexander 1922. [synonymy by Zwick 1990: 234].

Diagnosis.—Very small to moderately large blepharicerid. Larva: Cranium with deep lateral incisions, each extended anteriorly to include eyespots. Antenna two-segmented, usually with elongate intersegmental membrane. Dorsal prolegs absent (in some species, anterolateral margins of segments II–VI somewhat developed, simulating prolegs). Ventral gills in form of erect whorls, the number of filaments usually six or seven in instar IV. Pupa: Ovoid to elongate-ovoid in shape. Scutum mostly glabrous, integument of metathoracic and abdominal tergites usually densely papillose; cephalic, scutal, branchial, and alar sclerites non-papillose (most species). Respiratory organs erect, parallel, projected anteriorly nearly to plane of anterior margin; lamellae of respiratory organ lobate, rigid, parallel, inner two slightly to markedly smaller and thinner than outer two. Sharp marginal fold separates dorsal and ventral surfaces along entire circumference. Ventrolateral adhesive organ on each of abdominal segments IV–VI. Adult: Head usually dichoptic (male) to subholoptic (female); female eye usually with wide callis oculi and with dorsal division flattened dorsally and much larger than ventral division. Wing widest at middle or just beyond; membrane hyaline; venation typical of *Blepharicera*: radial sector two-branched, basal section of vein R_{4-5} atrophied, cell r4 sessile, vein M_2 and crossvein bm-cu absent. Legs slender, segments more or less straight, femora and tibiae slightly expanded distally, basitarsi moderately long; mid tibial spurs usually absent, hind pair usually present; mid coxa of female with setose median outgrowth; claws non-setate dorsally. *Male terminalia:* Epandrium (tergite IX) moderately sclerotized, subquadrate, simple, usually with setiform sensilla. Tergite X produced posteriorly as bilobed, variably hirsute cerci; shape varies among species. Hypoproct conical, membranous, often bearing 2–4 prominent setiform sensilla. Gonocoxites subrectangular, broadly fused with hypandrium (sternite IX) ventrolaterally; inner gonocoxal lobe glabrous, projecting posteriorly from inner base of gonocoxite. Gonostyli simple, deeply cleft to distinctly bilobed, variously set with microtrichia, hairs, and spiniform sensilla. Dorsal paramere platelike but thinly sclerotized in some species and with lateral thickenings or a posterodorsal sclerotization in other species; ventral parameres in form of two attenuate processes, the apices of which are simple to complex. Aedeagus of three slender filaments that arise from bulbous, basal sperm pump. *Female terminalia:* Tergite IX not expanded distolaterally, without stout setae. Sternite IX internally Y to T shaped (genital fork); stem of fork variously developed but arms usually prominent and sclerotized. Sternite X usually a sclerotized plate, sometimes with lateral extensions articulating with lower margins of tergite X. Spermathecae typically three in number, variable in shape; neck either simple (straight) or coiled.

Blepharicera tenuipes group Hogue 1978

Blepharicera tenuipes group Hogue 1978: 6 [original designation], Hogue 1987: 102 [review of Nearctic fauna].

Included species.—*Blepharicera*:
appalachiae Hogue and Georgian 1986
capitata Loew 1863
caudata, **new species**
chattooga, **new species**
cherokea Hogue 1978
corniculata, **new species**
coweetae Hogue and Georgian 1986
diminutiva Hogue 1978

gelida, **new species**
hispida, **new species**
magna, **new species**
separata Alexander 1963
similans Johannsen 1929
tenuipes (Walker) 1848
tuberosa, **new species**
williamsae Alexander 1953

Diagnosis.—Larva: Prolegs large, with wide base tapered to pointed apex; proleg largely visible from above; dorsal prolegs absent, represented instead by small setate convexity. Anal division usually broadly trilobate posteriorly; lateral lobes well developed, extended obliquely or posteriorly. Pupa: In most species, abdominal papillae small (width ≤ 10 μm) and bearing microscopic spinules apically; adjacent papillae separated by more than papilla width; integument of abdominal tergites often with micropunctures between papillae. Abdominal tergite IV usually more strongly expanded laterally than others. Adult: Head with ultimate antennal flagellomere slightly longer (1.2–1.6×) than penultimate flagellomere; penultimate flagellomere not diminutive. Ultimate palpal article longer (> 2×) than proximate article. Parietal setae few to numerous in female, rarely present in males. Male cerci well developed, prominent, parallel; interlobular depression deep; cercal lobes quadrate with various apical sublobes. Gonostyli simple, slightly concave on inner surface. Sperm sac bilobate, without internal spines. Ejaculatory apodeme a small, vertical flange. Ventral parameres broad, usually with ornate apices. Outer aedeagal filaments curved around hypopygeal muscles. Female hypogynial plate with short, broad lobes; spermathecal necks simple, without anterior curve.

Keys to Species of Appalachian *Blepharicera* (*B. tenuipes* Group)[1]

Instar IV Larvae

1. Lateral processes on anal division pointed apically (Figs. 1, 71, 73–74); body robust, large (instar IV > 6 mm) 2
– Lateral processes on anal division blunt apically (Figs. 2, 4, 7–8, 10, 12, 15, 72, 77); body usually small (< 6 mm) 3
2(1). Anal division acutely trilobed, medial lobe elongate and tapered apically (Figs. 1, 71) ..... *B. caudata*, n. sp.
– Anal division bluntly trilobed, the medial lobe never elongate (Figs. 73–74) ..... *B. magna*, n. sp.
3(1). One or two rows of prominent dorsal tubercles (Figs. 2–3, 15–16, 77, 124–128, 140–142) 4
– Dorsal tubercles absent (Figs. 4, 12–13, 72, 78–79, 97, 103–109, 110–111, 116–117, 132, 134) 6
4(3). Dorsum with row of small, submedian tubercles on each side (Figs. 15–16, 140–141); tubercles consist of an area of elongate-ellipsoid sensilla (Fig. 142); body coloration usually uniformly dark ..... *B. tuberosa*, n. sp.
– Dorsum with row of prominent, median tubercles, one per abdominal division (Figs. 2–3, 77, 124–128); body coloration either piebald or uniformly pale 5
5(4). Body coloration piebald (Fig. 77); dorsal secondary sensilla sparse, mostly clavate (Figs. 126–128) ..... *B. separata* Alexander
– Body coloration uniformly pale (yellow), except cranial sclerites (dark brown) (Fig. 80); dorsal secondary sensilla numerous, clavate and long setiform (Figs. 2–3, 124–125) .. *B. capitata* Loew
6(3). Clypeus w/ pair of prominent, anteriorly projected spines (Figs. 97–98); presently known only from Chattooga River ..... *B. corniculata*, n. sp.
– Clypeal spines absent 7
7(6). Dorsal secondary sensilla mostly setiform (Figs. 12–13, 104–105) 8
– Dorsal secondary sensilla mostly clavate (Figs. 10–11, 110–112) to globose (Figs. 132–135, 137) 9
8(7). Dorsal secondary sensilla short (shorter than first antennal segment) (Fig. 104) ..... *B. appalachiae* Hogue and Georgian

[1] Modified versions of these keys are available at http://www.ent.iastate.edu/dept/research/systematics/bleph/

– Dorsal secondary sensilla elongate (longer than first antennal segment) (Figs. 12–13) . . . . . *B. gelida*, n. sp.

9(7). Dorsal secondary sensilla mostly globose (Figs. 132–135) . . . . . *B. similans* Johannsen

– Dorsal secondary sensilla mostly clavate or digitiform (Figs. 10–11, 110–112) 10

10(9). Body and cranial sclerites uniformly colored (light to dark brown) 11

– Body and cranial sclerites usually with contrasting color patterns (Figs. 72, 78–79) 13

11(10). Substernal sensilla (adjacent to first suctorial disc) dark (Fig. 75); dorsal sensilla minute, about as long as broad (Figs. 8–9, 108); body small (instar IV < 5 mm) . . . . . *B. diminutiva* Hogue

– Substernal sensilla (adjacent to first suctorial disc) light, usually yellow (Fig. 76); dorsal sensilla well developed, usually dense, sometimes forming distinct clusters (Figs. 110–112); body large (instar IV > 5 mm) 12

12(11). Dorsal sensilla arranged in transverse anterior and posterior clusters (as in Fig. 109) . . . . . *B. tenuipes* (Walker)

– Dorsal sensilla densely distributed over segments, not arranged in distinct transverse clusters (Figs. 10–11, 110–112) . . . . . *B. hispida*, n. sp.

13(10). Ecdysial stem line short, frontoclypeal apotome reaching posterior margin of head capsule (Fig. 4); head capsule mottled or uniformly colored, with frontoclypeal apotome not noticeably darker than rest of head capsule (Fig. 72); membranous region of antenna much shorter than apical sclerotized region; presently known only from Chattooga River . . . . . *B. chattooga*, n. sp.

– Ecdysial stem line long basally, frontoclypeal apotome separated from posterior margin of head capsule (as in Fig. 133); frontoclypeal apotome typically darker than rest of head capsule; membranous region of antenna approximately the same length as apical sclerotized region (Fig. 2) 14

The remaining species can be very difficult to distinguish. The continuation of this key refers to typical specimens.

14(13). Cephalothorax, trunk, and prolegs mostly yellow but sometimes with dark highlights; cranial sclerites usually yellow but with dark frontoclypeal apotome; antenna long, total length greater than length of frontoclypeal apotome (Figs. 2, 106) . . . . . *B. cherokea* Hogue

– Cephalothorax, trunk, and prolegs mostly dark but with light highlights; cranial sclerites either uniformly dark or dark with light highlights (Figs. 78–79); antenna short, total length less than length of frontoclypeal apotome 15

15(14). Body coloration: dark medial band, with lateral margins extended onto dorsum of proleg; lateral muscle scars usually well inside the margins of these bands; pale crescentic band near apex of proleg (Fig. 79); cranial sclerites usually with contrasting color pattern, with anterior half dark and posterior half light; if cranial sclerites with only small light bands, these extend perpendicular to frontoclypeal apotome; dorsal sensilla arranged in transverse anterior and posterior clusters (Fig. 109) . . . . . *B. coweetae* Hogue and Georgian

– Body coloration: uniformly dark or, if with dark medial band, the lateral margins not extended onto the dorsum of proleg; lateral muscle scars at margins of these bands; apex of proleg without pale crescentic band (Fig. 78); if cranial sclerites with contrasting color pattern, light bands typically extend parallel to frontoclypeal apotome; dorsal sensilla arranged rather diffusely over segment, not in transverse anterior and posterior clusters . . . *B. williamsae* Alexander

PUPAE
(UNKNOWN IN *B. CAUDATA*)

1. Middle lamellae of respiratory organ narrow at base, width approximately half width of outer lamellae 2

– Middle lamellae of respiratory organ broad at base, width greater than half width of outer lamellae 5

2(1). Branchial sclerite densely covered with small papillae (Fig. 160); cephalic sclerite with pair of ridges extended dorsoventrally for nearly half its height (Fig. 161) . . . . . *B. diminutiva* Hogue

– Branchial sclerite without papillae (Fig. 136); cephalic sclerite without submedian ridges 3

3(2). Integument of abdominal tergites with minute, dark papillae bearing microscopic spinules apically (Figs. 93, 138, 139, 154–156); found early summer to fall . . . . . *B. chattooga*, n. sp. and *B. similans* Johannsen

– Integument of abdominal tergites without distinct papillae, but with minute, circular patches of spinules (Figs. 152–153); these patches may give the appearance of light-colored papillae or papillae surrounded by light-colored halo (Fig. 88); found spring to early summer 4

4(3). Integument of abdominal tergites with micropunctures between circular patches, surface luster somewhat dull (less so than in *B. williamsae*) (Figs. 143–144); abdominal tergites often with double row of small, submedian tubercles (remnants of larval tubercles) . . . . . *B. tuberosa*, n. sp.

– Integument of abdominal tergites glabrous between circular patches, surface luster shiny (Figs. 152–153); abdominal tergites without submedian tubercles . . . . . *B. cherokea* Hogue

5(1). Integument of abdominal tergites with fine, reticulate (areolate) pattern; surface luster of tergites and branchial sclerite very dull (Figs. 169–171) . . . . . *B. williamsae* Alexander

– Integument of abdominal tergites homogeneous or otherwise sculptured, no reticulate pattern; surface luster shiny on at least branchial sclerite (Figs. 89, 131, 146, 149, 154, 166) 6

6(5). Integument of abdominal tergites without papillae, but with minute, circular patches of spinules (as in Figs. 152–153); these patches may give appearance of light-colored papillae or papillae surrounded by light-colored halo (Fig. 89) . . . . . *B. corniculata*

– Integument of abdominal tergites with minute, dark or white papillae (Figs. 90–96) 7

7(6). Abdominal papillae appearing as white dots against a darker background (Figs. 86–87, 95) 8

– Abdominal papillae darker than background coloration (Figs. 90–94, 96) 9

8(7). Abdominal papillae large (≥10 μm), adjacent papillae separated by distance that approximates papilla width (Figs. 87, 157–159); anterior lamella of respiratory organ thick, broadly rounded apically (Fig. 14); large (>6 mm) . . . . . *B. gelida*, n. sp.

– Abdominal papillae small (≤10 μm), adjacent papillae separated by distance that typically exceeds papilla width (Figs. 95, 129–131); anterior lamella of respiratory organ broadly pointed apically (as in Fig. 17); relatively small (<6 mm) . . . *B. capitata* Loew and *B. separata* Alexander

9(7). Abdominal papillae in clusters of 2, 3, or more, arrangement most apparent lateral to muscle scars (Figs. 96, 146–147) . . . . . *B. appalachiae* Hogue and Georgian

– Abdominal papillae more or less evenly spaced, rarely forming clusters lateral to muscle scars (Figs. 90–92, 94, 114, 121, 150, 167) 10

10(9). Abdominal papillae large (≥10 μm), adjacent papillae separated by distance that approximates papilla width (Figs. 120–122); lamellae of respiratory organs thick, broadly rounded apically (Fig. 6); large (>6 mm) . . . . . *B. magna*, n. sp.

– Abdominal papillae small (≤10 μm), adjacent papillae separated by distance that typically exceeds papilla width (Figs. 91–92, 113–114, 149–150); lamellae of respiratory organs broadly pointed apically (as in Fig. 17); relatively small (<6 mm) 11

11(10). Integument of abdominal tergites with micropunctures between papillae, surface luster somewhat dull (less so than in *B. williamsae*) (Figs. 91–92, 113–115, 149–151) . . . . . *B. coweetae* Hogue and Georgian and *B. hispida*, n. sp.

– Integument of abdominal tergites mostly glabrous between papillae, surface luster shiny (Figs. 90, 166–167) . . . . . *B. tenuipes* (Walker)

Adult Males
(Unknown in *B. caudata*)

1. Dorsal and ventral eye division subequal in size (Figs. 29, 39) 2

– Dorsal division of eye much smaller than ventral division (Figs. 44, 49) 7

2(1). Inner margin of cercus convex or expanded (Figs. 31, 36, 58) 3

– Inner margin of cercus straight, neither convex nor expanded (Figs. 26, 41, 55) 5

3(2). Inner margin of cercus greatly expanded near base, reaching to or beyond midline (Fig. 58); southern Appalachians . . . . . *B. williamsae* Alexander

– Inner margin of cercus convex or expanded broadly near apex (Figs. 31, 36); mostly central or northern Appalachians 4

4(3). Posterior margin of cercus with small process near inner edge and prominent, triangular lobe near outer margin (Fig. 31); cercus and epandrium set with few, mostly short setae . . . *B. gelida*, n. sp.

– Posterior margin of cercus with elongate, pointed process near inner edge and more or less rectangular near outer margin (Fig. 36); cercus and epandrium set with numerous, elongate setae . . . . . *B. hispida*, n. sp.

5(2). Cercus with sparse setae, posterior margin relatively straight (Fig. 26); dorsal paramere opaque (Fig. 27) . . . . . *B. corniculata*, n. sp.
– Cercus densely set with long setae, posterior margin with pronounced lobe near inner edge (Figs. 41, 55); dorsal paramere with pigmented outer margin (Figs. 42, 61) 6
6(5). Posterior margin of cercus with elongate, medially directed hook near inner edge (Fig. 41); dorsal paramere without medial dorsal carina (Fig. 42) . . . . . *B. magna*, n. sp.
– Posterior margin of cercus with blunt, ventrally projected lobe near inner edge (Fig. 55); dorsal paramere with medial dorsal carina (Fig. 61) . . . . . *B. coweetae* Hogue and Georgian
7(1). Inner margin of cercus expanded (Figs. 65, 67) 8
– Inner margin of cercus straight, not expanded (Figs. 21, 46, 51, 53–54, 56–57) 9
8(7). Inner margin of cercus expanded evenly and broadly, apical margin slightly convex, making outer margin somewhat lobulate (Fig. 65); median aedeagal filament of approximately same length as lateral filaments (Fig. 66); apex of ventral parameres simple . . . . . *B. capitata* Loew
– Inner margin of cercus shallowly convex and expanded slightly near base, apical margin straight and contributing to somewhat obtuse angulate outer margin (Fig. 67); median aedeagal filament distinctly longer than lateral filaments (Fig. 68); apex of ventral parameres incurved, asymmetrically bifurcate . . . . . *B. similans* Johannsen
9(7). Cercal lobes narrow, elongate, and generally pointed apically (Figs. 46, 51) 10
– Cercal lobes relatively broad and generally truncated apically (Figs. 21, 53–54, 56–57) 11
10(9). Apical margin of cercal lobe with acutely pointed lobe medially (Fig. 51); apex of dorsal paramere deeply incised on either side of pronounced medial dorsal carina (Fig. 52) . . . . . *B. tuberosa*, n. sp.
– Apical margin of cercal lobe with broadly rounded inner corner (Fig. 46); apex of dorsal paramere entire on either side of weak, medial dorsal carina (Fig. 47) . . . . . *B. separata* Alexander
11(9). Apex of dorsal paramere deeply incised on either side of pronounced medial dorsal carina; apex of ventral parameres complex, with stout, dorsally recurved hook (Figs. 59, 63); medium sized (wing length 5–6 mm) 12
– Apex of dorsal paramere weakly incised or entire on either side of weak medial dorsal carina; apex of ventral parameres simple (Figs. 22, 60, 62); small (wing length 3–4 mm) 13
12(11). Posterior margin of cercus with pronounced, ventrally curved lobe apically (Fig. 57); scutum and thorax mostly yellowish to light brown . . . . . *B. tenuipes* (Walker)
– Posterior margin of cercus with indinstinct lobe near inner margin, giving appearance of small posteromedian notch (Fig. 53); scutum and thorax mostly dark brown . . . . . *B. appalachiae* Hogue and Georgian
13(11). Posterior margin of cercus without conspicuous lobes or processes (Fig. 56) . . . *B. diminutiva* Hogue
– Posterior margin of cercus with conspicuous, triangular lobe (Figs. 21, 54) 14
14(13). Posterior cercal lobe near medial margin (Fig. 54) . . . . . *B. cherokea* Hogue
– Posterior cercal lobe equidistant between medial and outer margin (Fig. 21) . . . . *B. chattooga*, n. sp.

Adult Females
(Unknown in *B. caudata*)

1. Two spermathecae, medial spermatheca vestigial (Fig. 70) . . . . . *B. similans* Johannsen
– Three spermathecae (Figs. 20, 25, 30, 35, 40, 45, 50, 69) 2
2(1). Ducts of lateral spermathecae sclerotized and pigmented near genital aperture (Fig. 69) . . . . . *B. capitata* Loew
– Ducts of spermathecae membranous and unpigmented for entire length (Figs. 20, 25, 30, 35, 40, 45, 50) 3
3(2). Dorsal and ventral eye divisions contiguous laterally, without callis oculi (Figs. 28, 38) 4
– Dorsal and ventral eye divisions separated by callis oculi (Figs. 23, 43, 48) 6
4(3). Distal palpomere long, length approximately equal to length of previous three palpomeres combined; number of parietal sensilla > 30; scutum and scutellum concolorous, except light rectangular patch just anterior to scutellum; scutellum with lateral sensilla distinctly clustered . . . . . *B. williamsae* Alexander
– Distal palpomere short, length approximately equal to length of previous two palpomeres combined (Figs. 28, 38); number of parietal sensilla usually five or fewer; scutellum distinctly lighter than scutum; scutellum with lateral sensilla arrangement diffuse 5
5(4). Scutum with short, setiform sensilla along prescutal suture and behind transverse suture . . . . . *B. magna*, n. sp.

– Scutum without short, setiform sensilla along prescutal suture and behind transverse suture . . . . . *B. gelida*, n. sp.
6(3). Callis oculi narrow (width approximately equal to diameter of dorsal ommatidium) 7
– Callis oculi broad (width equal to diameter of 2–3 dorsal ommatidia) 10
7(6). Distal palpomere long, length approximately equal to length of previous three palpomeres combined; number of parietal sensilla > 20 . . . . . *B. coweetae* Hogue and Georgian
– Distal palpomere short, length approximately equal to length of previous two palpomeres combined; number of parietal sensilla variable 8
8(7). Number of parietal sensilla 20 to 25 (Fig. 18) . . . . . *B. chattooga*, n. sp.
– Number of parietal sensilla usually 15 or fewer (Figs. 33, 43) 9
9(8). Posterior margin of trochanter with scattered, setiform sensilla; spermathecae ovoid (Fig. 35) . . . . . *B. hispida*, n. sp.
– Posterior margin of trochanter mostly glabrous, setiform sensilla only at base or apex; spermathecae pearshaped (Fig. 45) . . . . . *B. separata* Alexander
10(6). Distal palpomere short, length approximately equal to length of previous two palpomeres combined (Fig. 23); number of parietal sensilla 15 or fewer (Fig. 23) 11
– Distal palpomere long, length approximately equal to length of previous three palpomeres combined; number of parietal sensilla > 20 12
11(10). Scutum and thoracic pleurites dark brown to gray . . . . . *B. appalachiae* Hogue and Georgian
– Scutum and thoracic pleurites mostly pale posterior to anepimeron . . . . . *B. corniculata*, n. sp.
12(10). Number of parietal sensilla < 20 . . . . . *B. tuberosa*, n. sp.
– Number of parietal sensilla > 20 13
13(12). Abdominal tergites more or less concolorous . . . . . *B. tenuipes* (Walker)
– Most abdominal tergites (III and posteriorly) with anterior ⅓ somewhat lighter than posterior ⅔ 14
14(13). Posterolateral margin of sternite VIII with approximately 10 setiform sensilla, medial depression U shaped; medium-sized species (wing length usually > 5 mm) . . . . . *B. cherokea* Hogue
– Posterolateral margin of sternite VIII with no more than three setiform sensilla, medial depression V shaped; very small species (wing length < 5 mm) . . . . . *B. diminutiva* Hogue

Blepharicera appalachiae Hogue and Georgian 1986 (Figs. 53, 59, 82–83, 96, 104–105, 146–148, 172)

Blepharicera tenuipes "atypical" (southern type): Hogue 1978: 21 [taxonomic notes, figure of cerci].

"*Blepharicera* Larva C": Hogue 1978: 28 [description, collection records, figure].

"*Blepharicera* Larva E" (in part): Hogue 1978: 29 [description, collection records, figure].

Blepharicera appalachiae Hogue and Georgian 1986: 5 [original designation]; Hogue 1987: 103 [redescription, keys, figures]; Johns 1996: 2 [phenology]; Courtney 1998: 745 [rearing technique]; Alverson 2000: 20 [larval diets]; Courtney and Duffield 2000: 87 [in trout diets].

Diagnosis.—A medium-sized *Blepharicera*. Larva: Dorsal sensilla setiform or taeniaform, not arranged in clusters; cranial sclerites and body of uniform color, without pattern. Pupa: Ovoid in shape; integument of abdominal tergites shiny, gray to pale brown; papillae dark, irregularly arranged, typically coalesced into clusters of two or three; lamellae of respiratory organ of subequal width, broadly pointed apically. Adult male: Posterior margin of dorsal paramere deeply incised on either side of medial dorsal carina; dorsal eye division much smaller than lower; cercus with inner margin straight, posterior margin with conspicuous, triangular lobe near medial margin. Adult female: With 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; scutum and thoracic pleurites dark brown or gray.

Description.—See Hogue and Georgian (1986) and Hogue (1987).

Type material.—Holotype [male]: UNITED STATES. NORTH CAROLINA: *Macon Co:* Lower Shope Fork, Coweeta Hydrological

Laboratory, 35°03′N 83°26′W, 9 May 1981, coll. T. Georgian [LACM].

Collection localities [see Hogue and Georgian (1986) for additional sites].—UNITED STATES. GEORGIA: *Lumpkin Co:* Dicks Ck nr Waters Ck, 34°41′N 83°56′W; *Rabun Co:* Reed Mill Ck @ Rd 86, 34°56′N 83°11′W; West Fork Chattooga River, 34°57′N 83°12′W; *Towns Co:* Coleman R nr Tallulah R, 34°55′N 83°52′W; Tallulah R nr Tate Branch, 34°57′N 83°33′W; *Union Co:* Helton Ck below falls, 34°45′N 83°53′W; upper Nottley R nr Edwards Cove, 34°45′N 83°51′W; *White Co:* Chatahoochee R nr Martin Branch, 34°44′N 83°45′W; Dukes Ck @ FS Rd 244, 34°42′N 83°47′W; Smith Ck nr Anna Ruby Falls, 34°44′N 83°43′W; MARYLAND: *Frederick Co:* Big Hunting Ck, Catoctin Park, 39°37′N 77°26′W; Hauver Br, Cunningham Falls, 39°37′N 77°28′W; Owens Ck, Catoctin Mt Park, 39°39′N 77°26′W; NORTH CAROLINA: *Alleghany Co:* Little Glade Cr @ Blue Ridge Parkway, 36°27′N 81°00′W; Little R @ Sparta, 36°29′N 81°06′W; *Clay Co:* Big Tuni Ck 1mi above Tusquitee R, 35°06′N 83°41′W; Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W; Buck Ck nr confl Park Ck, 35°03′N 83°35′W; Fires Ck @ Picnic Area, 35°05′N 83°51′W; Hiwasee River, 35°03′N 83°53′W; *Graham Co:* Panther Ck, Nantahala NF, 35°23′N 83°37′W; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W; Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W; Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W; Chestnut Branch, GSMNP, 35°45′N 83°06′W; Cold Springs Ck, Pisgah NF, 35°44′N 83°01′W; Little Cataloochee Ck, GSMNP, 35°40′N 83°04′W; Palmer Ck, GSMNP, 35°38′N 83°08′W; *Henderson Co:* Mills R nr Pisgah boundary, 35°23′N 82°35′W; *Macon Co:* Big Buck Ck @ Hwy 64, 35°07′N 83°16′W; Curtis Ck @ FS Rd 67, 35°04′N 83°31′W; lower Ball Ck, CHL, 35°03′N 83°26′W; lower Dryman Fork, 35°02′N 83°24′W; lower Shope Fork, CHL, 35°03′N 83°26′W; Nantahala River nr Curtis Ck, 35°04′N 83°31′W; *McDowell Co:* Mill Ck @ Old Fort, 35°37′N 82°10′W; North Fork Catawba River, 35°48′N 82°01′W; *Swain Co:* Deep Ck, GSMNP, 35°27′N 83°26′W; Oconaluftee R, GSMNP, 35°32′N 83°17′W; Raven Fork, GSMNP, 35°31′N 83°17′W; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W; N Fk French Broad R, 35°13′N 82°51′W; *Yancey Co:* S Toe R @ Black Mountain, 35°45′N 82°13′W; SOUTH CAROLINA: *Oconee Co:* Chattooga R @ Hwy 76, 34°49′N 83°18′W; PENNSYLVANIA: *Bedford Co:* Scrubgrass Ck, 2mi W of Queens, 40°14′N 78°31′W; *Berks Co:* Willow Ck, Fleetwood watershed, 40°26′N 75°48′W; *Centre Co:* Galbraith Gap Run, 40°46′N 77°44′W; Spring Ck, Lemont Quarry, 40°48′N 77°48′W; *Pike Co:* Little Bushkill Ck SE of Tamiment, 41°08′N 75°00′W; Wallenpaupack Bk @ Rt 507, 41°19′N 75°18′W; trib [Mill Bk?], Lake Wallenpaupack [41°23′N 75°14′W]; *Schuylkill Co:* Locust Ck @ Rt 53036, 40°48′N 76°02′W; TENNESSEE: *Claiborne Co:* Powell R @ Indian Ck, 36°33′N 83°36′W; *Cocke Co:* Cosby Ck, GSMNP, 35°45′N 83°12′W; trib Cosby Ck, GSMNP, 35°45′N 83°12′W; *Johnson Co:* Beaverdam Ck @ Backbone, 36°35′N 81°49′W; Fagall Branch, 36°34′N 81°51′W; *Sevier Co:* Little Pigeon R, GSMNP, 35°44′N 83°24′W; Injun Ck nr Greenbrier, 35°43′N 83°24′W; trib Little Pigeon River, 34°57′N 83°12′W; VIRGINIA: *Bland Co:* Wolf Ck nr Bastion, 37°10′N 81°08′W; *Botetourt Co:* Jennings Ck @ Hwy 614, 37°32′N 79°37′W; North Fork CG, Jefferson NF, 37°32′N 79°35′W; *Craig Co:* small Ck along Hwy 621, Jefferson NF, 37°22′N 80°15′W; *Giles Co:* Stoney Ck nr White Rocks, 37°26′N 80°31′W; White Rocks Branch, 37°26′N 80°30′W; *Madison Co:* Cedar Run, Shenandoah NP, 38°32′N 78°21′W; White Oak Canyon, Shenandoah NP, 38°32′N 78°21′W; *Montgomery Co:* Craig Ck, Jefferson NF, 37°19′N 80°22′W; *Rappahannock Co:* Piney R, Shenandoah NP, 38°42′N 78°16′W; Hughes R, Shenandoah NP, 38°35′N 78°19′W; *Page Co:* Rapidan R, Shenandoah NP, 38°29′N 78°24′W; *Smyth*

Co: Nicks Ck @ SR 622, 36°49′N 81°25′W; *Washington Co:* S Fk Holston River, 36°39′N 81°50′W; Straight Creek, Mt Rogers, 36°38′N 81°43′W; WEST VIRGINIA: *Monroe Co:* trib S Fk Potts Ck @ NF boundary, 37°27′N 80°28′W; S Fk Potts Ck @ NF boundary, 37°27′N 80°28′W.

Distribution (Fig. 172).—*Blepharicera appalachiae* is widespread in streams of the southern and central Appalachian Mountains. In the northern part of its range (e.g., Blue Ridge of Virginia), *B. appalachiae* is usually the most abundant blephariceridae.

Bionomics.—*Blepharicera appalachiae* is collected most frequently during late spring and early summer, when larvae and pupae are common in many Appalachian streams. The species appears to be univoltine but with a relatively asynchronous emergence pattern. Although found mostly in mid-sized and moderately exposed streams, *B. appalachiae* inhabits a range of stream types. In the southern Appalachians, *B. appalachiae* can occur in relatively high flow (to 2 m/s) but is one of the few species to inhabit the lower current velocities of stream glides, riffle margins, or deeper habitats. In large rivers, the species frequently occurs on the same rocks that harbor *B. separata* (see below). In the central Appalachians, *B. appalachiae* occurs mostly in torrential habitats and often in densities exceeding 500 individuals/m^2 (Courtney, unpublished data). This species can be an important trout food in some Appalachian streams (Courtney and Duffield 2000).

Remarks.—Larval coloration is somewhat variable in certain populations. Although most individuals are brown or brownish yellow, some can be very pale or very dark. Regardless of their overall color, *B. appalachiae* larvae can be distinguished from most other species by chaetotaxy (setiforms distributed generally over trunk and prolegs) and by the lack of color patterns on the cephalothorax and body. These differences are somewhat less obvious in the northern part of the species' range, where *B. appalachiae* can be sympatric with *B. tenuipes*; however, *B. appalachiae* lacks the transverse clusters of sensilla that characterize larval *B. tenuipes*. In the southern Appalachians, adult *B. appalachiae* and *B. cherokea* sometimes are collected together. These species can be difficult to separate by genitalic characters (i.e., unless the parameres are removed and examined) but are easily distinguished by color differences (*B. appalachiae* scutum and thoracic pleurites uniformly dark brown or gray).

Blepharicera capitata Loew 1863
(Figs. 2–3, 65–66, 69, 80, 95, 124–125, 176)

Blepharocera sp.: Loew 1862: 8 [family diagnosis].

Blepharoptera capitata Loew 1863: 298. [original designation; genus name *lapsus calami* for *Blepharocera*].

Blepharocera capitata: Loew 1869: 87 [historical and taxonomic notes, adult keys], 1877: 62 [historical and taxonomic notes, adult keys]; Osten Sacken 1878a: 17 (in part) [synonymized with *B. tenuipes*], 1878b: 405 (in part) [historical and taxonomic notes, adult keys], 1891: 408 (in part) [review of family, adult keys], 1895: 150 (in part) [historical and taxonomic notes, adult keys]; Kellogg 1903: 197 (in part) [general descriptions, ecology]; Alexander 1953: 44 [taxonomic notes], 1958: 820 [species list].

"*Blepharocera tenuipes* (Walker)": Aldrich 1905: 172 (in part) [catalog]; Kellogg 1907: 12 (in part) [review of Nearctic fauna, adult keys], Kellogg 1908: 152 (in part) [review of Nearctic fauna, adult keys]; Alexander 1963: 50 (in part) [species list]. Incorrect synonymy by Osten Sacken 1878a.

"*Blepharicera tenuipes* (Walker)": Walley 1927: 113 (in part) [taxonomic notes].

Blepharicera capitata Loew: Stone 1965: 99 [catalog]; Hogue 1978: 9 [lectotype designation, redescription]; Hogue and Georgian 1986: 3 [taxonomic notes, adult keys]; Hogue 1987: 107 [redescription, adult keys].

"*Blepharicera capita* Loew": Carlson 1981: 68. [*lapsus calami* for *B. capitata*].

Diagnosis.—A small *Blepharicera*, very similar to *B. separata*. Larva: Stout, with prominent dorsal tubercles; body uniformly colored, pale yellow in most populations; dorsal sensilla mostly long setiforms or taeniaforms. Pupa: Delicate, pale, usually with small dorsomedial tubercles on abdominal segments I–VI; lamellae of respiratory organ of subequal width; abdomen with light-colored papillae evenly distributed on the dorsum. Adult male: Dorsal eye division much smaller than lower; cercus with inner margin expanded evenly and broadly, apical margin slightly convex, making outer margin somewhat lobulate; aedeagal filaments subequal in length and apex of ventral parameres simple. Adult female: 3 spermathecae, lateral 2 ducts distinctly sclerotized and pigmented at base; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere somewhat elongate (≈2× length of penultimate palpomere); number of parietal sensilla <10.

Description.—Larva (Figs. 2–3, 80, 124–125): Measurements, instar II (N = 10) total length 2.0 mm (1.6–2.4), cranial width 0.23 mm (0.21–0.25); instar III (N = 15) total length 3.1 mm (2.4–5.4), cranial width 0.35 mm (0.34–0.37); instar IV (N = 10) total length 4.8 mm (4.4–5.1), cranial width 0.45 mm (0.43–0.46), antennal segments 0.08 mm, 0.20 mm (0.18–0.23), membrane 0.10 mm. Larva stout, with prominent dorsal tubercles dorsomedially on each abdominal division. Cranial sclerites dark brown; ecdysial lines with abbreviated stem line; posterior margin of frontoclypeal apotome extended nearly to posterior cranial margin; clypeal spines absent. Trunk and prolegs uniformly colored, yellow to light brown. Anal division with posterior margin broadly convex, lateral processes poorly developed. Chaetotaxy: Cranial sclerites with scattered digitiforms; rest of cephalothorax and body generally covered with long, pale setiforms and taeniaforms, and a few short digitiforms; apex of median tubercles with stout, curved digitiforms; lateral lobe setiforms grading into digitiforms distally, but with numerous setiforms near apex; lateral lobes ventrally with few sensilla except clusters of setiforms apically; anal division with 6–8 prominent setiforms along apex of median lobe; substernal setae digitiform, yellow, 5–10 in number.

Pupa (Fig. 95): Measurements, male (N = 6) length 4.1 mm (3.9–4.2), width 2.5 mm (2.4–2.6); female (N = 6) length 4.5 mm (4.3–4.8), width 2.6 mm (2.5–2.7). Body roughly ovoid, somewhat dorsoventrally compressed. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments; few papillae on metatergite. Papillae light in color, with no or poorly developed spinules. Cuticle between papillae glabrous, uniform in structure and pigmentation. Branchial sclerite without papillae. Anal tergite smooth, unwrinkled. Middle lamellae of respiratory organ broad basally, width at midpoint greater than half width of outer lamellae.

Adult male and female: See Hogue (1987).

Type material.—Lectotype [female, designated by Hogue (1978)]: UNITED STATES. DISTRICT OF COLUMBIA: Washington, 1866, coll. C.R. Osten Sacken [MCZ].

Material examined.—UNITED STATES. GEORGIA: *Rabun Co:* Pine Mountain, 34°57′N 83°10′W, 15 May 1957 [A]; MARYLAND: *Cecil Co:* Octorara Canyon, 39°40′N 76°08′W, 17 June 1939 [A]; *Prince George's Co:* Beltsville, 39°02′N 76°53′W, 28 May 1916 [A]; NEW YORK: Sacandaga R, Sport Island [A]; NORTH CAROLINA: *Montgomery Co:* Little R @ Co Rd 1340, 35°23′N 79°49′W, 7–8 April 1995 [L]; PENNSYLVANIA: *Lebanon Co:* Ono [Swatara Ck, 40°23′N 76°33′W?], 7 June 1940 [A]; *Monroe Co:* Delaware Water Gap, 15 June 1934 [A]; *Pike Co:* Big Bushkill Ck, DWG, 41°05′N 75°00′W, 25 June 1995 [LP]; Dingmans Ck, Delaware Water Gap (DWG), 41°13′N 74°53′W, 25 June 1995 [P]; Little Bushkill

Ck, DWG, 41°05′N 75°00′W, 25 June 1995 [LP]; Raymondskill Ck, DWG, 41°17′N 74°50′W, 25 June 1995 [P]; SOUTH CAROLINA: *Oconee Co:* Chattooga R @ Hwy 76, 34°49′N 83°18′W, 26 April 1994 [LP], 4 March 1995 [L], 23 March 1995 [L], 5–6 April 1995 [LP], 15 March 1996 [L], 3 April 1996 [L], 21 April 1996 [L], 7 May 1996 [LP], 12 May 1996 [LP]; TENNESSEE: *Claiborne Co:* Powell R @ Indian Ck, 36°33′N 83°36′W, 10 April 1997 [L]; *Maury Co:* Duck R @ Hardison Mill Rd, 35°36′N 86°49′W, 26 March 1995 [P—identification tentative]; VERMONT: *Chittenden Co:* Smuggler's Notch, 44°33′N 72°47′W, 18 June 1927 [A]; *Windham Co:* [West?] Dummerston [42°55′N 72°36′W], 14 July 1908 [A]; VIRGINIA: *Fairfax Co:* Great Falls, 38°59′N 77°15′W, 21 June 1931 [A]; Trammel's Landing (= Riverbend County Park), 39°01′N 77°15′W, 28 May 1935 [A]; Turkey Run Park, 38°57′N 77°09′W, 27 May 1991 [A], 2 June 1991 [A].

Distribution (Fig. 176).—*Blepharicera capitata* is widespread in the central and southern Appalachians but seemingly rare. Except for certain collections from the Delaware Water Gap (e.g., Little Bushkill Creek) and the southern Appalachians (e.g., Chattooga River), most records consist of one or a few specimens.

Bionomics.—Collection records suggest that *B. capitata* is active primarily during the spring, especially in the southern Appalachians. At sites where this species and *B. separata* are sympatric (e.g., Chattooga River), *B. capitata* larvae are present as early as March. Here and elsewhere, *B. capitata* appears to be univoltine. Most collection records are from relatively large and predominantly low-gradient rivers. The presence of this species at some sites (e.g., lower Potomac River near Washington, D.C.) suggests that *B. capitata* is more tolerant of environmental impacts (e.g., sedimentation) than most *Blepharicera*.

Remarks.—Differences in the male genitalia of this species and *B. separata* prompted Hogue (1987) to question his earlier (Hogue 1978) synonymy of *B. separata* with *B. capitata*. The present analysis confirms that these species should be recognized as separate taxa. The most compelling evidence is the presence of distinct and consistent differences between sympatric populations at the Chattooga River. These differences help separate the larvae (chaetotaxy), adult males (cercal shape), and adult females (sclerotization of spermathecal ducts). Differences between pupae were not apparent, so the pupal description is based partly on collection date, dissection of pharate adults, and adult rearings.

Blepharicera caudata Courtney, new species
(Figs. 1, 71, 176)

Diagnosis.—A large *Blepharicera*. Larva: Anal tergite distinctly trilobed, the middle lobe elongate and tapered apically; lateral processes on abdominal segment VII pointed apically.

Description.—Larva (Figs. 1, 71): Measurements (N = 10): Total length 8.5 mm (7.7–10.4), cranial width 0.75 mm (0.70–0.85), antennal segments: 0.18 mm (0.15–0.20), 0.22 mm (0.21–0.25); membranous region 0.09 mm (0.08–0.10). Cranial sclerites dark brown to black; ecdysial lines with distinct stem line; posterior margin of frontoclypeal apotome not extended to posterior cranial margin; clypeal spines absent. Trunk dark brown to black; lateral lobes sometimes slightly lighter in color; prolegs dark brown to brownish orange. Anal division with posterior margin distinctly trilobed, middle lobe elongate and tapered apically; lateral lobes extended posteriorly and pointed at apex. Chaetotaxy: Digitiforms distributed generally over cephalothorax and body, dark in color; opaque/pale setiforms at apex of proleg; lateral lobes with sparse fusiforms ventrally; anal division with 4–6 prominent setiforms along apex of median lobe; substernal setae digitiform, pale brown, approximately 30 in number.

Pupa: Unknown.

Adult male: Unknown.

Adult female: Unknown.

Type material.—Holotype [instar IV larva]: UNITED STATES. NORTH CAROLINA: *Haywood Co:* GSMNP, Lost Bottom Creek, 35°38′N 83°08′W, 5 March 1997, coll. G.W. Courtney. Specimen in Canada balsam on slide [USNM]. Paratypes: Same data as holotype [10 instar IV L (1 slide, 9 EtOH)]; 12 April 1999 [1 instar IV L (EtOH)], coll. G.W. Courtney; Lost Bottom Creek @ upper falls, 35°38′N 83°08′W, 18 November 1992 [1 instar IV L (EtOH)], coll. H. Soehn and G. Salansky; Pretty Hollow Creek, 35°38′N 83°07′W, 5 March 1997 [1 instar IV L (EtOH)], coll. G.W. Courtney. Paratypes deposited in CUAC, GSMNP, ISU, and USNM.

Etymology.—From the Latin for tailed (*caudata*), in reference to the distinct anal division of the larva.

Distribution (Fig. 176).—*Blepharicera caudata* is apparently confined to the southeastern part of the Great Smoky Mountains. The species is currently known from only two sites, both third-order tributaries of Palmer Creek in the Cataloochee Creek drainage.

Bionomics.—Collection records suggest that *B. caudata* overwinters as a fourth-instar larva, emerges in early spring (April?), and exhibits a highly synchronous life history. The latter may at least partly explain the difficulty in locating pupae of this species. In 1997, March samples included several mature larvae (see type series), but April samples provide neither additional larvae nor pupae that were distinctly different from other species. The latter included more than 100 specimens, most assignable to *B. williamsae*. Attempts to collect additional material during 1998 were confounded by a January flood that scoured Lost Bottom Creek and other streams in the Smoky Mountains. Sampling at Lost Bottom Creek during March, 1998, provided numerous larval *B. williamsae* but no *B. caudata*. Because the hatching period of *B. williamsae* extends through January, its numbers might have been less impacted by the January flood. An April, 1999, collection provided only one additional larva. Nearly all *B. caudata* larvae were found on bedrock or large substrata and in currents exceeding 1.5m/s.

Remarks.—Although I am generally opposed to describing species based solely on immature stages, I have described *B. caudata* from only the larval stage. My reasons for this are threefold. First, *B. caudata* has perhaps the most distinctive larva of any Nearctic *Blepharicera*, so there is little chance it could be confused with other species. Second, I have successfully associated the larvae, pupae, and adults of all other *Blepharicera* from the area, so I am confident that the larvae of *B. caudata* do not develop into the pupae and adults of any known species. Finally, my attempts to locate pupae and adults of *B. caudata* have been confounded by logistics. I am hopeful that, by describing this species, someone based in the southern Appalachians might be compelled to search for and locate the pupae or adults of *B. caudata*. Until additional life stages are discovered, it will be difficult to establish with confidence the relationship between this species and other *Blepharicera*. The larvae share a number of features with *B. williamsae* (e.g., chaetotaxy, coloration). However, because many of the most distinctive characteristics of *B. williamsae* are in the pupal and adult stages, any suggested relationship with *B. caudata* is premature.

Blepharicera chattooga Courtney, new species

(Figs. 4–5, 18–22, 72, 93, 154–156, 172)

"*Blepharicera* sp. n. #10": Johns 1996: 2 [phenology].

Diagnosis.—A small *Blepharicera*. Larva: Dorsal secondary sensilla mostly clavate or digitiform; body with chevronlike or banded color pattern; cranial sclerites usually mottled, pattern corresponding with muscle scars; ecdysial stem line short; fron-

toclypeal apotome reaching posterior margin of cranium and not noticeably darker than rest of head. Pupa: Middle lamellae of respiratory organ narrow basally, width approximately half width of outer lamellae; integument of abdominal tergites with minute, dark papillae bearing microscopic spinules apically. Adult male: Dorsal eye division much smaller than lower; cercus with inner margin straight, posterior margin with conspicuous, triangular lobe that is equidistant between medial and outer margin. Adult female: 3 spermathecae with uniformly sclerotized and unpigmented ducts; dorsal and ventral eye divisions separated by narrow callis oculi; distal palpomere short (<3× length of penultimate palpomere); number of parietal sensilla 20–25.

Description.—Larva (Figs. 4, 72): Measurements, instar II (N = 3) total length 1.8 mm (1.5–1.9), cranial width 0.24 mm (0.23–0.25); instar III (N = 10) total length 3.2 mm (2.6–3.9), cranial width 0.38 mm (0.34–0.40); instar IV (N = 14) total length 4.6 mm (3.8–5.5), cranial width 0.59 mm (0.54–0.64), antennal segments: 0.12 mm (0.10–0.13), 0.18 mm (0.16–0.19); membranous region 0.05 mm (0.04–0.05). Cranial sclerites yellow, except interrupted by brown muscle scars; ecdysial lines with little to no stem line; posterior margin of frontoclypeal apotome extended nearly to posterior cranial margin; clypeal spines absent. Trunk light to dark brown, with pale ellipsoidal region along midline; lateral lobes generally darker than trunk but with lighter bands near base, a white patch on posterior margin, and a pale region at base of proleg. Anal division broadly trilobed, middle lobe with posterior margin truncate or slightly concave; lateral processes lobate, blunt at apex. Chaetotaxy: Cranial sclerite and cephalothorax with sparse claviforms; anterodorsal margin of each abdominal division with slight elevations bearing cluster of fusiforms; remaining trunk and lateral lobes with sparse fusiforms, grading to pale setiforms on proleg; proleg ventrally with few sensilla; anal division with 4 prominent setiforms along apex of median lobe; anal lobes each with 2 apical setiforms; substernal setae digitiform, pale yellow, 25–30 in number.

Pupa (Figs. 5, 93, 154–156): Measurements, male (N = 6) length 3.6 mm (3.4–3.8), width 2.0 mm (1.8–2.2); female (N = 10) length 4.1 mm (3.9–4.4), width 2.4 mm (2.2–2.5). Body outline roughly ellipsoid, broadly truncated anteriorly. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments; no papillae on metatergite, few on abdominal segment I. Papillae dark in color, with microspinules. Cuticle between papillae glabrous, uniform in structure and pigmentation. Branchial sclerite without papillae. Anal tergite smooth, unwrinkled. Middle lamellae of respiratory organ narrow basally, width at midpoint approximately half width of outer lamellae.

Adult male: Head and terminalia only (from dissected pupae):

Head (Fig. 19): Structure: Normal type, subholoptic. Clypeus length/width = 2.0. Eyes approximate dorsally, interocular distance approximately 0.07mm; eye divided, dorsal division much smaller than and contiguous with ventral division (callis oculi absent); dorsal division with approximately 10–12 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.34× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.1–1.1–5.0. Antenna with 15 articles, flagellomeres cylindrical; ultimate flagellomere 1.5× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but setose apically, f2–f12 setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; antennal coloration not determined (pharate). Chaetotaxy: Setiform groups as follows (number per side): clypeals (≈15), parietals (0), occipitals (≈10), verticals (2 or 3), postgenals (<10). Facial coloration not determined (pharate).

Terminalia (Figs. 21–22): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, weakly emarginate posteromedially, densely set with long, setiform sensilla. Cerci well developed, nearly parallel, densely set with long, setiform sensilla; interlobular depression narrowly U shaped; individual lobes broadly quadrate, inner margin straight, posterior margin with conspicuous, triangular lobe that is equidistant between medial and outer margins. Genital capsule small, longer than wide, posterolateral corners weakly produced. Gonostylus densely set with long, setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme elongate, extended approximately ⅔ distance to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere opaque, apex weakly incised or entire on either side of weak medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, slightly tapered to complex apex, with simple to slightly expanded medial margin; lateral parameral lobes large, broad, nearly parallel, with outer margins essentially straight.

Adult female: Head and terminalia only (from dissected pupae):

Head (Fig. 18): Structure: Normal type, subholoptic. Clypeus length/width = 2.1. Eyes approximate dorsally, interocular distance approximately 0.02 mm; eye divided, dorsal division subequal in size to and well separated from ventral division (callis oculi narrow); dorsal division with approximately 15 or 16 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.31× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.2–1.2–2.7. Antenna with 15 articles, flagellomeres cylindrical; ultimate flagellomere 1.8× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–12 with scattered setiforms, f13 setose basally and mostly glabrous apically but terminated in several prominent setiforms; scape and base of f1 pale yellow, pedicel and f1–13 concolorous, grayish brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (10–15), parietals (20–25), occipitals (≈20), verticals (2), postgenals (?). Facial coloration not determined (pharate).

Terminalia (Fig. 20): Posterior margin of sternite VIII broadly bilobate, medial depression prominent, broadly V shaped. Sternite IX (genital fork) broadly V shaped, with sclerotized extensions anteriorly and laterally. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves elongate, tapered slightly to broadly rounded apex; inner margins of valves slightly divergent. Accessory gland narrow, elongate, and extended beyond spermathecae basally, ovoid distally. Spermathecae 3 in number; corpora ovoid, slightly longer than wide, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII without prominent setiforms, but with 7 or 8 small, pale setiforms laterally; hypogynial plate and valves pruinose, set with minute setiforms; epiproct with 2–4 prominent setiforms apically.

Type material.—Holotype [pharate adult male, dissected from pupa]: UNITED STATES. SOUTH CAROLINA: *Oconee Co:* Chattooga River @ Hwy 76 Xing, 34°49′N 83°18′W, 13 July 1996, coll. G.W. Courtney. Specimen in Canada balsam on slide [USNM]. Allotype [pharate adult female, dissected from pupa]: same data as holotype; on slide [USNM]. Paratypes: Same locality as holotype: 18 June 1996 [5 instar IV L, 4 male P (EtOH)], coll. G.W. Courtney; 13 July 1996 [10 instar III L, 10 instar IV L, 10 female P (EtOH)], coll. G.W. Courtney; 2 August 1996 [10 instar IV L, 1 male P, 1 female P (EtOH)], coll. J.A. Johns. Paratypes deposited in CUAC, ISU and USNM.

Other material examined.—same locality

as type material: 2 May 1991 [L], coll. G.W. Courtney; 24 May 1994 [L], coll. P.H. Adler and J. McCreadie; 21 April 1995 [L], coll. J.A. Johns; 12 May 1995 [L], coll. G.W. Courtney; 17–19 May 1995 [L], coll. G.W. Courtney and J.A. Johns; 10 June 1995 [LP], coll. J.A. Johns; 5 July 1995 [P], coll. J.A. Johns; 21 July 1995 [LP], coll. J.A. Johns; 7 May 1996 [L], coll. J.A. Johns; 12 May 1996 [L], coll. J.A. Johns; 2 June 1996 [LP], coll. J.A. Johns; 7 June 1996 [L], coll. J.A. Johns; 18 June 1996 [LP], coll. G.W. Courtney; 2 July 1996 [P], coll. J.A. Johns; 13 July 1996 [LP], coll. G.W. Courtney; 2 August 1996 [LP], coll. J.A. Johns; 28 August 1996 [L], coll. P.H. Adler and E. Beard; 7 May 1997 [L], coll. G.W. Courtney; 13–14 May 1998 [LP], coll. A.J. Alverson and G.W. Courtney; 13 April 1999 [L], coll. G.W. Courtney.

Etymology.—The species is named after the type locality, the Chattooga River.

Distribution (Fig. 172).—*Blepharicera chattooga* is apparently confined to the Chattooga River, a fifth-order stream that forms the border between northwestern South Carolina and northeastern Georgia.

Bionomics.—The largest collections come from June and July, suggesting *B. chattooga* is primarily a summer species. However, larval collections ranging from early April to late August indicate a long period of activity and the possibility that *B. chattooga* is multivoltine. The species is largely sympatric with *B. similans*, both seasonally and in microhabitat characteristics. Larvae and pupae occur primarily in mainstream riffles where current velocities are relatively low (<1 m/s). Because *B. chattooga* adults have not been collected or observed in the field, nothing is known about their emergence patterns and behavior.

Remarks.—Pupae and adult females are nearly indistinguishable from *B. similans*, except that *B. chattooga* has three spermathecae (vs. two in *B. similans*). Larvae and adult males are somewhat more distinctive, largely because of subtle differences in color patterns, chaetotaxy, or [in males] terminalia. In spite of the similarities between these species, it is clear that they represent distinct taxa, especially as differences are consistent in areas of sympatry.

Blepharicera cherokea Hogue 1978
(Figs. 7, 54, 60, 88, 106–107, 152–153, 173)

Blepharicera cherokea Hogue 1978: 12 [original designation]; Georgian and Wallace 1983: 1237 (tentative identification) [larval diets]; Hogue and Georgian 1986: 3 [taxonomic notes, adult keys]; Hogue 1987: 110 [redescription, adult keys, figures]; Johns 1996: 2 [phenology]; Courtney 1998: 743 [rearing technique], 2000: 12 [figure of larval mouthparts].

Diagnosis.—A small to medium-sized *Blepharicera*. Larva: Dorsal secondary sensilla mostly clavate or digitiform; body usually uniformly colored, pale; ecdysial stem line long basally, frontoclypeal apotome separated from posterior margin of cranium and typically darker than rest of head. Pupa: Middle lamellae of respiratory organ narrow basally, width approximately half width of outer lamellae; abdominal tergites without papillae, but with small, circular patches of spinules; each patch usually surrounded by light-colored halo; integument between spinule patches glabrous. Adult male: Apex of dorsal paramere weakly incised on either side of weak medial dorsal carina; dorsal eye division much smaller than lower; cercus with inner margin straight, posterior margin with conspicuous, triangular lobe near medial margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla >20.

Description.—Larva (Figs. 7, 106–107): Measurements, instar IV (N = 26) total length 6.3 mm (4.5–7.9), cranial width 0.66 mm (0.57–0.72), antennal segments: 0.19

mm (0.10–0.26), 0.29 mm (0.20–0.38); membranous region 0.14 mm (0.08–0.20), approximately the same length as apical sclerotized region. Cranial color: Most individuals with yellow genae and brown frontoclypeal apotome; in larvae of some populations, cranium entirely yellow except for dark ecdysial lines; posterior part of genae sometimes with light brown muscles scars; ecdysial lines with distinct stem line; posterior margin of frontoclypeal apotome not extended to posterior cranial margin; clypeal spines absent. Antenna elongate, underside of distal article largely membranous. Trunk and lateral lobes mostly yellow to cream, uniformly colored; prolegs light brown. Lateral lobes tapered gradually and broadly at apex. Anal division with posterior margin broadly convex; prolegs moderately developed, straight laterally, blunt apically. Chaetotaxy: Cranial sclerites with scattered fusiforms; rest of cephalothorax and body generally covered with fusiforms, and few short digitiforms; lateral lobe fusiforms grading into setiforms distally, ventrally glabrous except for clusters of setiforms apically; proleg with numerous setiforms at apex; anal division with 8–10 prominent setiforms along apex of median lobe; substernal setae digitiform, yellow, approximately 20 in number.

Pupa (Figs. 88, 152–153): Measurements, male (N = 19) length 4.0 mm (3.4–4.4), width 2.2 mm (1.8–2.4); female (N = 20) length 4.6 mm (4.2–5.2), width 2.5 mm (2.2–2.9). Body outline roughly ellipsoid, broadly truncated anteriorly. Integument: Abdominal tergites set with "false papillae" consisting of circular patches of spinules; under light microscope, each spinule patch may have appearance of light-colored papilla or papilla surrounded by light-colored halo; patches uniformly distributed on abdominal segments; relatively few papillae present on metatergite. Cuticle between spinule patches glabrous, uniform in structure and pigmentation. Branchial sclerite without papillae or spinule patches. Anal tergite wrinkled. Middle lamellae of respiratory organ narrow basally, width at midpoint approximately half width of outer lamellae.

Adult male and female: See Hogue (1987).

Type material.—Holotype [male]: UNITED STATES. NORTH CAROLINA: *Macon Co:* Highlands, Clear Creek, 3,200 feet, 1–2 July 1958, coll. J.G. Franclemont [CUI].

Collection localities.—UNITED STATES. GEORGIA: *Dawson Co:* Amicalola Falls, 34°33′N 84°15′W; *Rabun Co:* Reed Mill Ck @ Rd 86, 34°56′N 83°11′W; West Fork Chattooga River, 34°57′N 83°12′W; *Towns Co:* Tallulah R nr Tate Branch, 34°57′N 83°33′W; NORTH CAROLINA: *Clay Co:* Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W; Buck Ck nr confl Park Ck, 35°03′N 83°35′W; Fires Ck @ FS Rd 340A, 35°06′N 83°50′W; Fires Ck @ Picnic Area, 35°05′N 83°51′W; Leatherwood Falls, 35°05′N 83°51′W; Park Ck nr confl Buck Ck, 35°03′N 83°35′W; Rock House Ck nr Fires Ck, 35°06′N 83°50′W; *Graham Co:* Little Santeetlah Ck @ Joyce Kilmer, 35°21′N 83°55′W; Panther Ck, Nantahala NF, 35°23′N 83°37′W; Sand Ck @ FS Rd 81, 35°20′N 83°58′W; Santeetlah Ck @ FS Rd 81, 35°20′N 83°54′W; Santeetlah Ck nr Wright Ck, 35°20′N 83°56′W; trib Santeetlah Ck, 35°20′N 83°56′W; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W; Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W; Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W; Chestnut Branch, GSMNP, 35°45′N 83°06′W; Cold Springs Ck, Pisgah NF, 35°44′N 83°01′W; Little Cataloochee Ck, GSMNP, 35°40′N 83°04′W; Lost Bottom Ck, GSMNP, 35°38′N 83°08′W; Palmer Ck, GSMNP, 35°38′N 83°08′W; W Fk Pigeon R @ "falls", 35°20′N 82°54′W; W Fk Pigeon R @ Sunburst, 35°22′N 82°56′W; *Macon Co:* Bearpen Ck @ Rd 67, 35°02′N 83°30′W; Bearpen Ck @ Rd 67, 35°02′N 83°30′W; Clear Ck up FS Rd 79C, 35°00′N 83°12′W; Curtis Ck @ FS Rd 67, 35°04′N 83°31′W; Hemp Patch Ck @ FS Rd 67, 35°01′N 83°30′W; Hurricane Ck @ FS Rd 67, 35°03′N 83°30′W; Jarrett Ck @ Rd 437,

35°09′N 83°37′W; lower Ball Ck, CHL, 35°03′N 83°26′W; lower Dryman Fork, 35°02′N 83°24′W; lower Shope Fork, CHL, 35°03′N 83°26′W; N Fk Cold Springs Cove, 35°01′N 83°26′W; Nantahala River nr Curtis Ck, 35°04′N 83°31′W; Roaring Fk @ Rd 437, 35°07′N 83°36′W; Shope Fk @ Rd 7276, CHL, 35°03′N 83°27′W; trib Jarrett Ck, Wayah Bald, 35°09′N 83°36′W; upper Dryman Fork, CHL, 35°02′N 83°26′W; Wayah Ck nr Rd 388, 35°09′N 83°32′W; *McDowell Co:* Curtis Ck near CG, 35°41′N 82°11′W; trib Curtis Ck above Licklog, 35°42′N 82°11′W; *Swain Co:* Bryson City, 35°26′N 83°26′W; Cherokee, Soco Valley, 35°28′N 83°18′W; Deep Ck, GSMNP, 35°27′N 83°26′W; Oconaluftee R, GSMNP, 35°32′N 83°17′W; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W; N Fk French Broad R, 35°13′N 82°51′W; SOUTH CAROLINA: *Oconee Co:* Brasstown Falls, 34°43′N 83°18′W; Chattooga R @ Hwy 76, 34°49′N 83°18′W; trib Brasstown Ck, 34°43′N 83°18′W'; *Pickens Co:* Rocky Bottom Ck @ Rt 178, 35°02′N 82°48′W; TENNESSEE: *Cocke Co:* trib Cosby Ck, GSMNP, 35°45′N 83°12′W; *Sevier Co:* Greenbrier Cove, GSMNP, 35°42′N 83°23′W; Injun Ck nr Greenbrier, GSMNP, 35°43′N 83°24′W; Little Pigeon R, GSMNP, 35°44′N 83°24′W; Porters Ck @ trailhead, GSMNP, 35°41′N 83°23′W; trib Little Pigeon River, GSMNP, 34°57′N 83°12′W.

Distribution (Fig. 173).—Although Hogue (1987) believed this species was endemic to the type locality and nearby streams, *B. cherokea* is among the most widespread and locally abundant species in the southern Appalachians. The species is particularly common in the southern Blue Ridge and Smoky Mountains, and is expected from streams farther south and west in Georgia, Tennessee, and perhaps northern Alabama.

Bionomics.—*Blepharicera cherokea* is primarily an early spring species, hatching in March or April at most sites. Larvae that hatch early often overlap temporally with mature larvae of the winter species *B. coweetae, B. magna,* and *B. williamsae.* Phenological data suggest that most populations of *B. cherokea* are univoltine and have relatively synchronous emergence and development. Although recorded from a wide variety of streams, *B. cherokea* occurs primarily in small- to medium-sized (third- and fourth-order) streams. This is one of the few species that frequents streams with a closed canopy or extensive riparian cover. Most larval and pupal habitats also are characterized by moderately high current velocity (>1 m/s). Adults are common in riparian vegetation, where they often rest on the undersides of leaves.

Remarks.—Larvae show considerable variation in color, especially in pigmentation of cranial sclerites. In most individuals, the frontoclypeal apotome is dark and the body, cephalothorax, and genal sclerites are yellow. However, variation in the pigmentation of the frontoclypeal apotome and adjacent cuticle can make some *B. cherokea* difficult to distinguish from other species, particularly lighter individuals of *B. coweetae* and darker individuals of *B. similans.* In these instances, chaetotaxy is the most reliable taxonomic character. Pupae of *B. cherokea* can be quite variable in size, but are readily identified by a suite of characters (middle lamellae of respiratory organ narrow basally; abdominal tergites with small patches of spinules surrounded by light-colored halos, and glabrous cuticle between patches).

Blepharicera corniculata Courtney, new species

(Figs. 23–27, 89, 97–98, 103, 172)

"*Blepharicera* sp. n. #4": Johns 1996: 2 [phenology].

Diagnosis.—A medium-sized *Blepharicera.* Larva: Prominent anteriorly projected, clypeal spines. Pupa: Abdominal tergites with poorly developed papillae, but with circular patches of spinules; each patch surrounded by light-colored halo; minute fur-

rows or punctures between spinule patches; lamellae of respiratory organ of subequal width, broadly rounded apically. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin straight, posterior margin without prominent lobes. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere short (<3× length of penultimate palpomere); number of parietal sensilla 10–15.

Description.—Larva (Figs. 97–98, 103): Measurements, instar IV (N = 10): total length 5.7 mm (4.4–6.2), cranial width 0.59 mm (0.56–0.62), antennal segments 0.13 mm (0.12–0.15), 0.18 mm (0.17–0.20), membrane 0.05 mm. Cranial sclerites mostly dark brown to black, without pattern but some individuals with light brown/yellow patch adjacent to eyespot (similar to *B. tuberosa, B. coweetae*); ecdysial lines with short stem line, frontoclypeal apotome nearly reaches posterior cranial margin; clypeal spines present, usually light brown. Trunk dark brown to black; lateral lobes taper gradually to proleg base, truncate apically. Anal division with posterior margin rounded; anal prolegs moderately developed, triangular. Chaetotaxy: Cranial sclerites largely glabrous, with few short fusiforms; cephalothorax and body with scattered short fusiforms and digitiforms, dark in color; opaque to pale setiforms at apex of lateral lobes and proleg; lateral lobes ventrally with sparse chaetiforms near proleg base; anal division with 4–6 prominent setiforms along apex of median lobe; substernal setae digitiform, pale brown, approximately 15 in number.

Pupa (Fig. 89): Measurements, male (N = 10) length 4.5 mm (4.2–4.8), width 2.6 mm (2.4–2.9); female (N = 10) length 5.1 mm (4.7–5.4), width 2.9 mm (2.7–3.1). Body outline roughly ellipsoid, broadly truncated anteriorly. Integument: Abdominal tergites set with "false papillae" consisting of circular patches of spinules (similar to *B. cherokea*); under light microscopy, each spinule patch may give appearance of light-colored papilla or papilla surrounded by light-colored halo; patches uniformly distributed on abdominal segments; a few spinule patches present on metatergite. Cuticle homogeneous, without reticulate pattern but with minute furrows or punctures between spinule patches. Branchial sclerite without papillae. Anal tergite wrinkled. Middle lamellae of respiratory organ broad basally, width at midpoint greater than half width of outer lamellae.

Adult male: Head and terminalia only (from dissected pupae):

Head (Fig. 24): Structure: Normal type, subholoptic. Clypeus length/width = 2.1. Eyes approximate dorsally, interocular distance approximately 0.06 mm; eye divided, dorsal division contiguous with ventral (callis oculi absent) and subequal in size to ventral division, with approximately 16 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.30× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.1–1.1–4.3. Antenna with 15 articles, flagellomeres cylindrical; ultimate flagellomere 1.3× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but setose apically, f2–f12 setose, f13 setose basally and mostly glabrous apically but terminated in several prominent setiforms; scape, pedicel, and base of f1 brownish yellow, remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (≈10), parietals (0), occipitals (≈15), verticals (3), postgenals (≈15). Facial coloration not determined (pharate).

Terminalia (Figs. 26–27): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, weakly emarginate posteromedially, set with numerous long, setiform sensilla. Cer-

ci well developed, nearly parallel, sparsely set with setiform sensilla; interlobular depression U shaped; individual lobes broadly quadrate, inner margin straight, posterior margin relatively straight to slightly sinuate. Genital capsule small, about as wide as long, posterolateral corners strongly produced. Gonostylus with numerous setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme elongate, extended approximately ⅔ distance to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere opaque, apex weakly incised on either side of medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, slightly tapered to apex; apex of ventral parameres simple to slightly curved laterally; lateral parameral lobes large, broad, with outer margins divergent and somewhat emarginate.

Adult female: Head and terminalia only (from dissected pupae):

Head (Fig. 23): Structure: Normal type, subholoptic. Clypeus length/width = 2.5. Eyes approximate dorsally, interocular distance approximately 0.03 mm; eye divided, dorsal division subequal in size to and well separated from ventral division (callis oculi broad); dorsal division with 15 or 16 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.50× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.1–1.1–3.2. Antenna with 15 articles, flagellomeres cylindrical, slightly wider near base; ultimate flagellomere 1.6× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–12 with scattered setiforms, f13 setose basally and mostly glabrous apically but terminated in several prominent setiforms; scape, pedicel, and base of f1 brownish yellow, remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (15–20), parietals (10–15), occipitals (≈20), verticals (3), postgenals (≈15). Coloration: Frons, face and clypeus grayish brown, pruinose.

Terminalia (Fig. 25): Posterior margin of sternite VIII broadly bilobate, medial depression prominent, broadly U shaped. Sternite IX (genital fork) broadly U shaped, most specimens without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves elongate, subrectangular; inner margins of valves parallel, outer margins slightly divergent. Accessory gland elongate, narrow, wrinkled anteriorly, terminating near spermathecae, not obviously expanded in most specimens. Spermathecae 3 in number; corpora ovoid, slightly longer than wide, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII with 4–6 prominent setiforms laterally and few short setiforms medially; hypogynial plate and valves pruinose, set with minute setiforms; epiproct with two or three prominent setiforms apically.

Type material.—Holotype [pharate adult male, dissected from pupa]: UNITED STATES. SOUTH CAROLINA: *Oconee Co:* Chattooga River @ Hwy 76 Xing, 34°49′N 83°18′W, 12 May 1995, coll. G.W. Courtney. Specimen in Canada balsam on slide [USNM]. Allotype [adult female, reared]: same locality as holotype, 12 May 1995, coll. G.W. Courtney; emerged 15 May. Specimen pinned, genitalia in glycerin [USNM]. Paratypes: same locality as holotype: 24 May 1994 [3 female P (slides)], coll. P.H. Adler; 12 May 1995 [9 instar IV L (EtOH), 1 male P (slide), 12 female P (EtOH)], coll. G.W. Courtney; 7 May 1997 [2 instar IV L, 2 male P, 1 female P (EtOH)], coll. G.W. Courtney; 14 May 1998 [1 male P, 3 female P (slides)], coll. G.W. Courtney; 13 April 1999 [6 instar III L, 15 instar IV L (EtOH)], coll. G.W. Courtney. Paratypes deposited in CUAC, ISU and USNM.

Other material examined.—Same data as holotype: 2 May 1991 [L], coll. G.W.

Courtney; 26 April 1994 [LP], coll. G.W. Courtney; 4 May 1994 [LP], coll. J.A. Johns; 24 May 1994 [P], coll. P.H. Adler and J. McCreadie; 23 March 1995 [L], coll. J.A. Johns; 6 April 1995 [L], coll. J.A. Johns; 21 April 1995 [L], coll. J.A. Johns; 12 May 1995 [LP], coll. G.W. Courtney; 17–19 May 1995 [LP], 7 May 1996 [L], coll. J.A. Johns; 7 May 1997 [LP], coll. G.W. Courtney; 14 May 1998 [LP], A.J. Alverson and G.W. Courtney; 13 April 1999 [L], coll. G.W. Courtney.

Etymology.—From the Latin for "horned" (*corniculatus*), in reference to the two spinelike tubercles on the larval clypeus.

Distribution (Fig. 172).—*Blepharicera corniculata* is apparently endemic to the Chattooga River, a fifth-order stream that forms the border between northwestern South Carolina and northeastern Georgia.

Bionomics.—Larvae and pupae of *B. corniculata* typically occur on large substrata in moderately high current velocities (>1 m/s). They also may frequent thin films of water flowing over large rocks and bedrock (e.g., madicolous zones). Larval records range from late March (early instars) to mid-May, with the largest collections from late April to early May. Phenological data from the Chattooga River suggest that *B. corniculata* is univoltine and exhibits fairly synchronous egg hatching and development. Adult *B. corniculata* have not been observed in the field, and rearings have been nearly impossible because pupation sites are primarily on large substrata, which can not be removed and transported to a lab. Consequently, nothing is known about adult emergence patterns and behavior.

Remarks.—The unusual clypeal structure (prominent anteriorly projected spines) make larval *B. corniculata* one of the most distinctive blepharicerids. In other respects the larvae are very similar to *B. coweetae*. Pupae most closely resemble those of *B. cherokea*, but can be distinguished by the relatively broad middle lamellae of the respiratory organs. Adult males are less easily separated from several other medium-sized species (*B. hispida*, *B. coweetae*), but can be recognized by cercal shape. Females do not appear to have any distinguishing characteristics, being one of several species with a relatively short distal palpomere and eyes separated by a broad callis oculi.

Blepharicera coweetae Hogue and Georgian 1986
(Figs. 55, 61, 79, 91, 109, 149–151, 173)

Blepharicera coweetae Hogue and Georgian 1986: 9 [original designation]; Hogue 1987: 113 [redescription, keys, figures]; Johns 1996: 2 [phenology]; Courtney 1998: 743 [rearing technique].

Diagnosis.—A medium-sized *Blepharicera*. Larva: Dorsal secondary sensilla mostly fusiforms, arranged in two broad, transverse bands medially; color variable but typically with contrasting cranial pattern, anterior half dark and posterior half light; body with dark medial band, its lateral margins extended onto dorsum of lateral lobes; lateral muscle scars well inside margins of these bands; pale crescentic band near apex of lateral lobe. Pupa: Ovoid in shape; integument of abdominal tergites glabrous; papillae dark, uniformly spaced, with minute furrows or punctures between papillae; lamellae of respiratory organ of subequal width, broadly rounded apically. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin straight, posterior margin with pointed lobe near medial margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by narrow callis oculi; distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla >20.

Description.—See Hogue and Georgian (1986) and Hogue (1987).

Type material.—Holotype [adult male]: UNITED STATES. NORTH CAROLINA: *Macon Co:* Lower Shope Fork, Coweeta Hy-

drological Laboratory, 35°03′N 83°26′W, 5 May 1984, coll. T. Georgian [LACM].

Collection localities.—UNITED STATES: GEORGIA: *Lumpkin Co:* Dicks Ck nr Waters Ck, 34°41′N 83°56′W; *Towns Co:* Coleman R nr Tallulah R, 34°55′N 83°52′W; Tallulah R nr Tate Branch, 34°57′N 83°33′W; *Union Co:* Helton Ck below falls, 34°45′N 83°53′W; *White Co:* Chattahoochee R nr Martin Branch, 34°44′N 83°45′W; Dukes Ck @ FS Rd 244, 34°42′N 83°47′W; NORTH CAROLINA: *Clay Co:* Big Tuni Ck 1mi above Tusquitee R, 35°06′N 83°41′W; Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W; Fires Ck @ FS Rd 340A, 35°06′N 83°50′W; Fires Ck @ Picnic Area, 35°05′N 83°51′W; *Graham Co:* Panther Ck, Nantahala NF, 35°23′N 83°37′W; Santeetlah Ck @ FS Rd 81, 35°20′N 83°54′W; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W; Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W; Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W; Little Cataloochee Ck, GSMNP, 35°40′N 83°04′W; Palmer Ck, GSMNP, 35°38′N 83°08′W; *Macon Co:* Cullasaja R nr Goldmine Rd, 35°05′N 83°15′W; lower Shope Fork, CHL, 35°03′N 83°26′W; *Madison Co:* spring Ck @ Rocky Bluff, 35°51′N 82°50′W; *McDowell Co:* North Fork Catawba River, 35°48′N 82°01′W; *Swain Co:* Deep Ck, GSMNP, 35°27′N 83°26′W; Oconaluftee R, GSMNP, 35°32′N 83°17′W; Raven Fork, GSMNP, 35°31′N 83°17′W; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W; N Fk French Broad R, 35°13′N 82°51′W; *Yancey Co:* Neals Ck @ FS Rd 2074, 35°44′N 82°12′W; SOUTH CAROLINA: *Oconee Co:* Brasstown Falls, 34°43′N 83°18′W; Chattooga R @ Hwy 76, 34°49′N 83°18′W; Chauga R @ Stumphouse Rd, 34°47′N 83°12′W; *Pickens Co:* Eastatoe Ck, 35°03′N 82°48′W. TENNESSEE: *Johnson Co:* Beaverdam Ck @ Backbone, 36°35′N 81°49′W; *Monroe Co:* Tellico R nr Ranger Station, 35°20′N 84°13′W; *Sevier Co:* Porters Ck @ trailhead, GSMNP, 35°41′N 83°23′W; VIRGINIA: *Washington Co:* S Fk Holston River, 36°39′N 81°50′W; Straight Creek, Mt Rogers, 36°38′N 81°43′W.

Distribution (Fig. 173).—Hogue and Georgian (1986) recorded *B. coweetae* "from a[n] . . . area about 17 km in diameter" (pg. 16) and believed the species was endemic to streams only in the Little Tennessee River drainage. However, *B. coweetae* is perhaps the most widespread of the southern Appalachian endemics. Current records range from northeastern Georgia and northwestern South Carolina, throughout western North Carolina, and northward to the Mount Rogers area of southwestern Virginia. The species probably occurs throughout northern Georgia and perhaps into northern Alabama. In some streams of North and South Carolina, *B. coweetae* is the most abundant blepharicerid during early spring.

Bionomics.—*Blepharicera coweetae* occurs primarily in small- to medium-sized (third and fourth order) streams and is sometimes abundant at well-shaded sites. Larval and pupal habitats are characterized by moderately high current velocity (>1 m/s). Phenological data suggest that most populations are univoltine but relatively asynchronous in egg hatching and development. As one of three winter species (Johns 1996) in the southern Appalachians, *B. coweetae* eggs may begin hatching in December and larval development can be nearly completed by early April. At many sites, this species and *B. williamsae* overlap seasonally and in microhabitat characteristics; however, sites with this sympatric combination typically are characterized by a numerical dominance of one or the other species (i.e., rarely do both species occur in high numbers).

Remarks.—The larvae of *B. coweetae* are among the most difficult to characterize, partly because of striking color variation. In most individuals, cranial sclerites are dark with yellow patches adjacent to the eyespots, a pattern seen also in many larvae of *B. williamsae*. At sites where these species co-exist, larvae can be separated only by

subtle differences in chaetotaxy and trunk color (see key couplet 15). In a few populations (e.g., Chattooga River), larvae can be almost uniformly yellow and closely resemble those of *B. cherokea*. Again, subtle differences in chaetotaxy are the primary method of separating these species. Although geographically isolated, *B. coweetae* and *B. tenuipes* can be difficult to separate; larvae differ mostly in coloration (*B. coweetae* usually with contrasting color patterns) and pupae differ only slightly (*B. coweetae* with micropunctures between abdominal papillae). Pupae of *B. coweetae* are indistinguishable from those of *B. hispida*. Adults of these species are also difficult to separate. Although less apparent in previous renderings (cf. fig. 160 in Hogue [1987]), the male cerci of *B. coweetae* often have a pronounced, ventrally curved lobe apically, making them quite similar to the cerci of *B. gelida, B. hispida* and *B. tenuipes*. In addition, the dorsal parameres of all species have a well-developed medial dorsal carina. Among this group of species, *B. tenuipes* is perhaps the most distinctive, due partly to the small, dorsal eye division and the deep incisions on the dorsal paramere. The remaining species can be separated by subtle differences in genitalic structure.

Blepharicera diminutiva Hogue 1978
(Figs. 8–9, 56, 62, 75, 85, 102, 108, 160–165, 172)

Blepharicera diminutiva Hogue 1978: 14 [original designation]; Hogue and Georgian 1986: 3 [taxonomic notes, adult keys]; Hogue 1987: 117 [redescription, adult keys, figures]; Johns 1996: 2 [phenology]; Courtney 2000: 25 [figure of adult head].

Diagnosis.—A small *Blepharicera*. Larva: Prominent dark substernal sensilla; dorsal sensilla minute (barely visible), about as long as broad; body and cranial sclerites uniformly colored (light to dark brown). Pupa: Branchial sclerite densely covered with small papillae; cephalic sclerite with pair of submedian ridges extended dorsoventrally for nearly half height of sclerite. Adult male: Dorsal division of eye much smaller than ventral division; cercus broader than long, with inner margin straight, posterior margin without prominent lobe medially, outer corner acutely rounded, extended posteriorly beyond inner corner. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla >20.

Description.—Larva (Figs. 8–9, 75, 102, 108): Measurements, instar III (N = 4): total length 3.4 mm (3.0–3.9), cranial width 0.38 mm (0.35–0.40); instar IV (N = 15): total length 4.8 mm (3.7–6.2), cranial width 0.55 mm (0.50–0.60), antennal segments 0.22 mm (0.20–0.23), 0.26 mm (0.25–0.28), membrane 0.05 mm. Cranial sclerites usually dark brown to black, without pattern; if patterned, posterodorsal region of genae and posterior half of frontoclypeal apotome dark and area medial to eyespots pale; ecdysial lines with short stem line; clypeal spines absent. Trunk uniformly dark brown to cream; if latter, then dorsum of trunk darker than lateral lobes and prolegs. Anal division with posterior margin truncate; anal prolegs moderately developed, triangular. Chaetotaxy: Cranial sclerites largely glabrous, with few short fusiforms, and rows of setiforms near labral margin; cephalothorax and body with scattered, short fusiforms, dark in color; opaque/pale setiforms at apex of lateral lobes and proleg; lateral lobes ventrally with sparse chaetiforms near proleg base; anal division with 4–6 prominent setiforms along apex of median lobe; substernal setae digitiform, dark brown, approximately 40 in number.

Pupa (Figs. 85, 160–165): Measurements, male (N = 15) length 3.5 mm (3.1–4.0), width 1.8 mm (1.7–2.0); female (N = 20) length 4.1 mm (3.6–4.4), width 2.1 mm (1.9–2.3). Body outline roughly ellipsoid, broadly truncated anteriorly. Integument:

Dorsal papillae present, uniformly dispersed on abdominal segments and metatergite. Papillae dark in color, relatively large, mushroomshaped, with minute spinules. Cuticle homogeneous, without reticulate pattern. Branchial sclerite densely covered with papillae anteriorly and laterally; cephalic sclerite with pair of submedian ridges extended dorsoventrally for a length of nearly half the height of the sclerite; alar sclerite markedly rugose laterally. Anal tergite wrinkled. Middle lamellae of respiratory organ very narrow, width less than half width of outer lamellae.

Adult male and female: See Hogue (1987).

Type material.—Holotype [male]: UNITED STATES. NORTH CAROLINA: *Macon Co:* Highlands, Clear Creek, 3,200 feet, 1 July 1958, coll. J.G. Franclemont [CUI].

Material examined.—UNITED STATES. GEORGIA: *Rabun Co:* Addie Branch, E Fk Chattooga R [presumably the tributary of Holcomb Ck, which flows into the W Fk Chattooga R], 34°58′N 83°15′W, 1 August 1957 [A]; Rabun Bald, 34°58′N 83°18′W, 14 July 1957 [A]; Tallulah Falls, 34°44′N 83°24′W, 10 June 1910 [A]; NORTH CAROLINA: *Clay Co:* Leatherwood Falls, 35°05′N 83°51′W, 20 May 1995 [LP], 8 July 1995 [LP]; *Haywood Co.* W Fk Pigeon R @ "falls", 35°20′N 82°54′W, 19 July 1995 [LPA], 14 July 1996 [LP]; *Macon Co:* Clear Ck up FS Rd 79C, 35°00′N 83°12′W, 29 May 1995 [L]; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W, 25 May 1995 [P]; Lake Toxaway, 35°07′N 82°56′W, 12 July 1957 [A]; SOUTH CAROLINA: *Oconee Co:* Brasstown Falls, 34°43′N 83°18′W, 17 May 1995 [L], 26 May 1995 [LPA], 29 May 1995 [LPA], 19 July 1995 [LP], 29–30 July 1995 [LP)], 16 August 1995 [LP], 14 May 1998 [LP], 12 September 1998 [LP]; Chattooga R @ Hwy 76, 34°49′N 83°18′W, 12 May 1998 [L]; *Pickens Co:* Green Ck, Table Rock trail, 35°02′N 82°42′W, 30 July 1995 [LP].

Distribution (Fig. 172).—Although collected from relatively few streams in the southern Appalachians, *B. diminutiva* can be locally abundant. Existing records include a small area in western North Carolina to northeastern Georgia and northwestern South Carolina. The species probably occurs at most waterfalls in the region.

Bionomics.—*Blepharicera diminutiva* occurs primarily in small (third order) streams with waterfalls; however, it is noticeably absent from the headwater seeps and waterfalls that harbor *B. williamsae*. In microhabitat characteristics, *B. diminutiva* is probably the most specialized eastern blepharicerid. Larval and pupal habitats consist almost exclusively of waterfall splash zones or madicolous habitats, both of which are characterized by thin films of flowing water. Phenological data from most populations suggest a univoltine life history; however, data from Brasstown Falls, South Carolina, (records from mid-May to mid-September) provide compelling evidence for a multivoltine pattern. Alternatively, the Brasstown population could have markedly asynchronous egg hatching and development. Although considered primarily a spring species (Johns 1996), *B. diminutiva* at Brasstown co-occurs temporally with *B. similans* and may qualify as a summer species. Despite temporal overlap at many sites, these species usually occur in different microhabitats. Adult *B. diminutiva* have been observed on several occasions at Brasstown Falls. In most instances adults were on riparian vegetation (e.g., *Acer, Alnus*), usually resting on the undersides of leaves. Concurrent collections have included *B. williamsae,* and on one occasion a female *B. williamsae* was observed feeding on a male *B. diminutiva.* When captured, the female had decapitated and pierced the abdomen of the male. These observations apparently represent the first record of an adult net-winged midge consuming another blepharicerid.

Remarks.—*Blepharicera diminutiva* is one of the most distinctive and least morphologically variable blepharicerids from the southern Appalachians. Larvae show slight varia-

tions in cranial and trunk color but, otherwise, are easily recognized by chaetotaxy (e.g., dark substernal sensilla and sparse fusiforms on dorsum). Pupae are even more distinctive, being the only Nearctic *Blepharicera* with papillae on the branchial sclerites. Adults are less easily distinguished from several other small species (*B. cherokea, B. separata*), but obvious genitalic differences permit separation of males.

Blepharicera gelida Courtney, new species

(Figs. 12–14, 28–32, 86–87, 157–159, 174)

"*Blepharicera* sp.": Courtney 2000: 8 [figure of larva].

Diagnosis.—A large *Blepharicera*. Larva: Stout, uniformly colored, brown or gray in most populations, covered with long, setiform sensilla. Pupa: Integument of abdominal tergites with micropunctures between light-colored papillae; lamellae of respiratory organ of subequal width, broadly rounded apically. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin expanded broadly near apex, posterior margin with small process near medial edge and broadly triangular lobe near outer margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions contiguous (callis oculi absent); distal palpomere short (<3× length of penultimate palpomere); number of parietal sensilla <5; hypogynial valves with distinct shape.

Description.—Larva (Figs. 12–13): Measurements, instar IV (N = 18) total length 5.9 mm (4.0–8.7), cranial width 0.65 mm (0.60–0.75), antennal segments 0.10 mm (0.10–0.12), 0.20 mm (0.19–0.22), membrane 0.05 mm. Cranial sclerites usually dark brown, without pattern (muscle scars distinct in some specimens); ecdysial lines with short stem line; posterior margin of frontoclypeal apotome nearly extended to cranial margin; clypeal spines absent. Trunk uniformly light brown to cream; if latter, then dorsum of abdominal segments II–IV darker than lateral lobes, and prolegs light brown. Anal division with posterior margin broadly truncate; lateral processes poorly developed. Chaetotaxy: Densely set with stout setiforms; cephalothorax and body with numerous stout setiforms, dark in color; opaque/pale setiforms at apex of lateral lobes and prolegs; lateral lobes ventrally glabrous; anal division with 15–20 prominent setiforms along apex of median lobe; substernal setae digitiform, dark brown, approximately 10 in number.

Pupa (Figs. 14, 86–87, 157–159): Measurements, male (N = 14) length 6.0 mm (5.8–6.2), width 3.9 mm (3.6–4.3); female (N = 17) length 6.7 mm (6.0–7.4), width 4.2 mm (3.6–4.7). Cuticle dark brown; body outline broadly oval. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments and metatergite. Papillae light in color, relatively large, with minute spinules; gaps between papillae subequal to papilla width. Cuticle homogeneous, without reticulate pattern. Branchial sclerite without papillae. Anal tergite smooth, unwrinkled. Respiratory lamellae black to dark brown; middle lamellae broad, width at midpoint greater than half width of outer lamellae.

Adult male: Size: Large. Measurements (N = 3): Total length 6.6 mm (6.4–6.7), wing length 7.3 mm (7.1–7.5), width 2.4 mm (2.3–2.5). Leg-segment lengths: Femora only (remaining segments stuck in pupal cases): foreleg 4.0–4.1 mm, midleg 4.1–4.2 mm, hindleg 5.1–5.3.

Head (Fig. 29): Structure: Normal, subholoptic. Clypeus length/width = 2.3. Eyes approximate dorsally, interocular distance approximately 0.09 mm; eye divided, dorsal division subequal in size to and contiguous with ventral division (callis oculi absent); dorsal division with approximately 23 rows of ommatidia along mid-meridian. Free portion of proboscis about 0.40× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions

1.0–1.4–1.2–3.0. Antenna with 15 articles, flagellomeres barrelshaped, most nearly as broad as long; ultimate flagellomere 1.4× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but setose apically, f2-f12 setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape pale, pedicel and flagellomeres brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (≈5), parietals (0), occipitals (≈15), verticals (3 or 4), postgenals (≈10).

Thoracic chaetotaxy: Scutum with approximately 15 chaetiforms posterolaterally; scutellum with cluster of 15–20 chaetiforms laterally and few scattered chaetiforms across midline.

Coloration: Frons, face and clypeus mostly pale to light brown; ocellar triangle dark brown to black. Thorax pruinose; mesoscutum mostly brown but pale around borders and "sutures"; scutellum pale; pleuron mostly pale, except katepisternum light brown. Forecoxae light brown, other coxae pale. Abdominal tergites uniformly brown, sternites and pleural membrane pale.

Terminalia (Figs. 31–32): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, emarginate posteromedially, set with short setiform sensilla. Cerci well developed, generally parallel; set with numerous, short setiform sensilla; interlobular depression hourglass-shaped; individual cercal lobes elongate, inner margin expanded broadly near apex, posterior margin emarginate, with small process near inner edge and prominent, triangular lobe near outer margin. Genital capsule small, slightly longer than wide, posterolateral corners strongly produced. Gonostylus set with numerous setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme elongate, extended approximately ⅔ distance to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere opaque, apex weakly emarginate either side of medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, slightly tapered to complex apex with slight hook on inner wall; lateral parameral lobes large, broad, with outer margins divergent and slightly emarginate.

Adult female: Size: Large. Measurements (N = 1 [allotype]): Total length 7.9 mm, wing length 8.8 mm, width 2.7 mm.

Leg-segment lengths:	foreleg	midleg	hindleg
femur	5.0	4.8	6.7
tibia	4.2	4.4	6.0
tarsus 1	2.0	2.0	2.6
2	1.0	1.0	0.9
3	0.6	0.6	0.6
4	0.5	0.5	0.5
5	0.5	0.5	0.5

Head (Fig. 28): Structure: Normal holoptic. Clypeus length/width = 2.7. Eyes approximate dorsally, interocular distance approximately 0.09 mm; eye divided, dorsal division subequal in size to and well differentiated from ventral division (but callis oculi absent laterally); dorsal division with approximately 24 rows of ommatidia along mid-meridian. Free portion of proboscis about 0.54× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.0–1.2–2.2. Antenna with 15 articles, flagellomeres barrelshaped; ultimate flagellomere 1.5× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–12 with scattered setiforms, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape and base of f1 brownish yellow, pedicel and remaining flagellomeres concolorous, dark brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (<5), parietals (0–2), occipitals (20–25), verticals (≈5), postgenals (0).

Thorax and appendages: Tibial spurs 0–0–2; spurs asymmetrical, one each long (0.25 mm) and short (0.11 mm); base of hind tarsomere 1 with cluster of 5 or 6 dark, spiniform sensilla. Leg-segment proportions: fore—36:30:14:7:4:4:4, mid—35:32:14:7:4:4:4, hind—38:34:15:5:3:3:3. Chaetotaxy: Scutum with approximately 15 chaetiforms posterolaterally; scutellum with cluster of 15–20 chaetiforms laterally and few scattered chaetiforms across midline.

Coloration: Frons and face dark brown to gray, clypeus brown. Thorax pruinose; mesoscutum light brown; scutellum pale; pleuron light brown anteriorly (episternum, anterior margin of anepimeron), pale posteriorly. Forecoxae light brown, other coxae pale. Abdominal tergites uniformly brown, sternites and pleural membrane pale.

Terminalia (Fig. 30): Posterior margin of sternite VIII broadly bilobate, medial depression prominent, U shaped. Sternite IX (genital fork) broadly U shaped, without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves narrow basally, expanded medially, tapered to blunt apex posteriorly; inner margins of valves parallel basally, divergent posteriorly. Accessory gland narrow, elongate, and extended beyond spermathecae basally, ovoid distally. Spermathecae 3 in number; corpora ovoid, wider than long, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII with ≈10 setiforms laterally and few short setiforms medially; hypogynial plate and valves pruinose, set with numerous minute and 2 slightly larger setiforms; epiproct with 2 prominent setiforms apically.

Type material.—Holotype [adult male, reared]: UNITED STATES. VIRGINIA: *Bland Co:* Wolf Creek nr Bastion, 37°10′N 81°08′W, 14 April 1999, coll. G.W. Courtney, emerged 26 April. Specimen pinned, genitalia in glycerin [USNM]. Allotype [adult female, reared]: same data as holotype; pinned, genitalia in glycerin [USNM]. Paratypes: same data as holotype, 2 January 1997 [3 instar IV L (EtOH)], coll. P.H. Adler; 14 April 1999 [4 male P, 4 female P (EtOH)], coll. G.W. Courtney; WEST VIRGINIA: *Greenbrier Co:* Greenbrier R below Renick, 37°59′N 80°21′W, 15 April 1999 [1 reared male A (pinned)], coll. G.W. Courtney; *Pocahontas Co:* Greenbrier R nr Seebert, 38°07′N 80°10′W, 30 December 1994 [6 instar IV L (EtOH)], coll. P.H. Adler; 8 March 1995 [7 instar IV L (EtOH)], coll. G.W. Courtney; 9 May 1995 [1 reared male A (pinned), 1 male and 1 female P (EtOH), 4 male and 1 female P (slides)], coll. G.W. Courtney. Paratypes deposited in ISU and USNM.

Other material examined.—UNITED STATES. TENNESSEE: *Claiborne Co:* Powell River @ Indian Creek, 36°33′N 83°36′W, 10 April 1997 [P], coll. C.N. Watson, Jr.; VIRGINIA: *Bland Co:* Wolf Creek nr Bastion, 37°10′N 81°08′W, 14 April 1999 [P], coll. G.W. Courtney; WEST VIRGINIA: *Greenbrier Co:* Greenbrier R below Renick, 37°59′N 80°21′W, 15 April 1999 [P], coll. G.W. Courtney; *Pocahontas Co:* Greenbrier R nr Seebert, 38°07′N 80°10′W, 8 March 1995 [L], coll. G.W. Courtney; 9 May 1995 [P], coll. G.W. Courtney.

Etymology.—From the Latin for "cold" (*gelidus*), in reference to the season of activity of this species.

Distribution (Fig. 174).—Although most records are from the Greenbrier River, collections from Tennessee and Virginia suggest that *B. gelida* is relatively widespread in the central and southwestern Appalachians. Focused sampling efforts during the winter and early spring should lead to additional records of this species.

Bionomics.—*Blepharicera gelida* is primarily an inhabitant of large rivers, where larvae and pupae frequent deep riffles in moderately high current velocity (>1 m/s). Collection records from the Greenbrier River and Wolf Creek suggest that most populations are univoltine and relatively synchronous in egg hatching and development. *Blepharicera gelida* is one of two winter species in the central Appalachians. Eggs apparently

begin hatching in late fall and larval development is nearly completed by late March. At all sites, this species and *B. hispida* show broad seasonal and microhabitat overlap; however, the latter occurs in much higher densities than does *B. gelida*.

Remarks.—Larvae of *B. gelida* are distinct, characterized by their large size, robust body, uniform coloration, and dense covering of elongate setiform sensilla. Pupae are similar to *B. magna* in overall shape and size, but possess light-colored abdominal papillae. Adult males and females resemble those of the smaller *B. hispida*, but differ in genitalic characteristics.

Blepharicera hispida Courtney, new species

(Figs. 10–11, 33–37, 92, 110–115, 175)

Diagnosis.—A medium-sized *Blepharicera*. Larva: Dorsal secondary sensilla digitiform and densely distributed over segments, not arranged in clusters. Pupa: Abdominal tergites with micropunctures between dark papillae; lamellae of respiratory organ of subequal width, broadly pointed apically. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin expanded broadly near apex, posterior margin with elongate, pointed process near medial edge and broadly quadrate outer margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by narrow callis oculi; distal palpomere relatively short (<3× length of penultimate palpomere); number of parietal sensilla ≈10.

Description.—Larva (Figs. 10–11, 110–112): Measurements, instar II (N = 1): total length 3.0 mm, cranial width 0.3 mm; instar III (N = 10): total length 4.1 mm (3.4–4.9), cranial width 0.41 mm (0.36–0.44); instar IV: [Greenbrier River] (N = 15) total length 6.2 mm (4.2–7.5), cranial width 0.65 mm (0.60–0.70), antennal segments 0.15 mm (0.13–0.18), 0.25 mm (0.23–0.28), membrane 0.09 mm; [S Br Middlebury River] (N = 10) total length 6.5 mm (5.4–7.4), cranial width 0.63 mm (0.60–0.66), antennal segments 0.10, 0.26 mm (0.23–0.30), membrane 0.08. Cranial sclerites light to dark brown, without pattern except lateral clypeal sclerite pale; ecdysial lines with long stem line; posterior margin of frontoclypeal apotome well removed from cranial margin; clypeal spines absent. Cephalothorax, trunk, lateral lobes and prolegs brown to dark brown. Anal division with posterior margin broadly rounded, never elongate; lateral process bluntly rounded apically. Chaetotaxy: Head, cephalothorax, and body densely set with brown elongate-fustiform sensilla; opaque/pale setiforms at apex of proleg; lateral lobes ventrally with scattered light brown fustiforms; anal division with 4–6 prominent setiforms along apex of median lobe; substernal setae fustiform, pale brown, 30–35 in number.

Pupa (Figs. 92, 113–115): Measurements, male: Wolf Creek (N = 25): total length 5.2 mm (4.6–5.6), width 3.1 mm (2.9–3.4); female: Wolf Creek (N = 25): total length 6.1 mm (5.5–6.4), width 3.5 mm (3.1–3.9); S Br Middlebury R (N = 10): total length 5.2 mm (4.8–5.5), width 3.0 mm (2.8–3.2). Cuticle dark brown; body outline generally ovoid. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments; metatergite with numerous papillae medially, none laterally. Papillae dark, with minute spinules; gaps between papillae exceed papilla width. Cuticle homogeneous, without reticulate pattern but with minute furrows or punctures between papillae. Branchial sclerite without papillae. Anal tergite wrinkled. Respiratory lamellae black to dark brown; middle lamellae broad, width at midpoint greater than half width of outer lamellae.

Adult male: Size: Medium. Measurements (N = 5): Total length 5.4 mm (5.0–6.0), wing length 6.0 mm (5.6–6.5), width 1.8 mm (1.7–1.9).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	3.4 (3.2–3.6)	3.6 (3.3–3.7)	4.9 (4.6–5.1)
tibia	3.1 (2.9–3.4)	2.9 (2.8–3.0)	4.4 (4.1–4.7)
tarsus 1	1.8 (1.7–1.9)	1.7 (1.6–1.8)	1.8 (1.6–2.0)
2	0.9 (0.8–1.1)	0.9 (0.8–1.0)	0.6 (0.6–0.7)
3	0.6 (0.6–0.7)	0.6 (0.6–0.7)	0.4
4	0.3 (0.3–0.4)	0.3 (0.3–0.4)	0.3 (0.2–0.3)
5	0.3 (0.3–0.4)	0.3 (0.3–0.4)	0.3 (0.2–0.3)

Head (Fig. 34): Structure: Normal, subholoptic. Clypeus length/width = 1.9. Eyes approximate dorsally, interocular distance approximately 0.05 mm; eye divided, dorsal division subequal in size to and contiguous with ventral division (callis oculi absent along boundary); dorsal division with 20–22 rows of ommatidia along mid-meridian. Free portion of proboscis about 0.35× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.2–1.2–4.0. Antenna with 15 articles, flagellomeres filiform; ultimate flagellomere 1.2× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but setose apically, f2-f12 densely setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape pale, pedicel and flagellomeres dark brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (5 or 6), parietals (≈10), occipitals (≈30), verticals (5 or 6), postgenals (20–25).

Thorax and appendages: Tibial spurs 0–0–1; base of hind tarsomere 1 with two or three dark, spiniform sensilla. Leg-segment proportions: fore—33:30:17:9:6:3:3, mid—35:28:17:9:6:3:3, hind—39:35:14:5:3:2:2. Chaetotaxy: Scutum glabrous; scutellum with cluster of 20–25 chaetiforms laterally and diffuse row of chaetiforms across midline.

Coloration: Frons and face dark brown, pruinose; clypeus mostly light brown to brown; ocellar triangle dark brown. Thorax pruinose; mesoscutum and scutellum brown; pleuron mostly brown anteriorly (episternum, anterior margin of anepimeron), pale posteriorly. Forecoxae brown, other coxae pale. Abdominal tergites light brown to brown, sternites pale to light brown, pleural membrane pale.

Terminalia (Figs. 36–37): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, slightly emarginate posteromedially, densely set with setiform sensilla. Cerci well developed, parallel; densely set with setiform sensilla; interlobular depression narrowly U shaped; individual cercal lobes elongate, inner margin convex near apex, posterior margin slightly emarginate, with prominent hook near inner edge and bluntly rectangular near outer margin. Genital capsule small, somewhat longer than wide, posterolateral corners strongly produced. Gonostylus densely set with setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme elongate, extended approximately ⅔ distance to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere opaque, apex weakly emarginate on either side of medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, tapered to complex apex with slight hook on inner wall; lateral parameral lobes large, broad, outer margins slightly divergent and emarginate.

Adult female: Size: Medium. Measurements (N = 2): Total length 6.7 mm (6.6–6.8), wing length 6.9 mm (6.8–7.0), width 2.0 mm.

Leg-segment lengths:	foreleg	midleg	hindleg
femur	3.9 (3.8–4.0)	3.9 (3.8–4.0)	5.6
tibia	3.4 (3.3–3.5)	3.2	5.0
tarsus 1	1.6	1.8	2.2
2	1.0	1.0	0.9
3	0.6	0.6	0.5
4	0.4	0.3	0.3
5	0.4	0.3	0.4

Head (Fig. 33): Structure: Normal holoptic. Clypeus length/width = 2.0. Eyes approximate dorsally, interocular distance approximately 0.04 mm; eye divided, dorsal division subequal in size to and well differentiated from ventral division (callis oculi narrow); dorsal division with 18–20 rows of ommatidia along mid-meridian. Free portion of proboscis about 0.52× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.3–1.2–2.7. Antenna with 15 articles, flagellomeres filiform; ultimate flagellomere 1.6× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–12 with scattered setiforms, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape and base of f1 light brown, pedicel and remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (10–15), parietals (≈10), occipitals (≈20), verticals (3–5), postgenals (≈20)

Thorax and appendages: Tibial spurs 0–0–2; spurs asymmetrical, one each long (0.3 mm) and short (0.05 mm); base of hind tarsomere 1 with two or three dark, spiniform sensilla. Leg-segment proportions: fore—35:30:14:9:5:4:4, mid—35:29:16:9:5:3:3, hind—38:34:15:6:3:2:3. Chaetotaxy: Scutum glabrous; scutellum with cluster of 20–25 chaetiforms laterally and diffuse row of chaetiforms across midline.

Coloration: Frons and face dark brown to gray, clypeus brown. Thorax pruinose; mesoscutum and scutellum uniformly brown; pleuron brown anteriorly (episternum, anterior margin of anepimeron), pale posteriorly. Forecoxae light brown, other coxae pale. Abdominal tergites light brown, anterior third and thin band near posterior margin slightly lighter in color; sternites light brown, pleural membrane pale.

Terminalia (Fig. 35): Posterior margin of sternite VIII broadly bilobate, medial depression prominent, broadly U shaped. Sternite IX (genital fork) broadly Y shaped, without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves elongate, subrectangular; inner margins of valves parallel, outer margins slightly divergent. Accessory gland narrow, elongate, and extended beyond spermathecae basally, ovoid distally. Spermathecae 3 in number; corpora circular, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII with 3–6 setiforms laterally and few short setiforms medially; hypogynial plate and valves pruinose, set with numerous minute setiforms; epiproct with two or three prominent setiforms apically.

Type material.—Holotype [adult male, reared]: UNITED STATES. WEST VIRGINIA: *Greenbrier Co:* Greenbrier R below Renick, 37°59′N 80°21′W, 15 April 1999, coll. G.W. Courtney, emerged 25 April. Specimen pinned, genitalia in glycerin microvial [USNM]. Allotype [adult female, reared]: same data as holotype; pinned, genitalia in glycerin microvial [USNM]. Paratypes: VERMONT: *Addison Co:* Green Mountain NF: S Br Middlebury R @ FS Rd 32 Xing, 43°56′N 72°59′W, 17 May 1996 [10 instar IV L (EtOH)], coll. G.W. Courtney; VIRGINIA: *Bland Co:* Wolf Creek nr Bastion, 37°10′N 81°08′W, 14 April 1999 [12 male and 10 female P (EtOH)], coll. G.W. Courtney; WEST VIRGINIA: same data as holotype [13 male and 8 female P (EtOH), 5 male and 5 female A (reared, EtOH), 15 male and 5 female A (reared, pinned)], coll. G.W. Courtney; *Pocahontas Co:* Greenbrier River nr Seebert, 38°07′N 80°10′W, 30 December 1994 [1 instar II and 10 instar III L (EtOH)], coll. P.H. Adler; 8 March 1995 [30 instar IV L (EtOH), 2 instar IV L (slides)], coll. G.W. Courtney; 9 May 1995 [2 female P (EtOH), 2 male and 3 female P (slides)], coll. G.W. Courtney. Paratypes deposited in AMNH, ISU, and USNM.

Other material examined.—UNITED STATES. NEW HAMPSHIRE: *Carroll Co:* Saco River above Sawyer Rock, 44°04′N 71°19′W, 23 June 1995 [Pex], coll. G.W. Courtney; Swift River above lower falls,

44°00′N 71°15′W, 18 May 1996 [L], coll. G.W. Courtney; Swift River below covered bridge, 44°00′N 71°14′W, 23 June 1995 [Pex], coll. G.W. Courtney; *Coos Co:* Zealand River @ Sugarloaf Trail, 44°15′N 71°30′W, 20 June 1991 [Pex], coll. G.W. Courtney; 23 June 1995 [P], coll. G.W. Courtney; 31 May 1998 [P], coll. A.J. Alverson and G.W. Courtney; *Grafton Co:* Baker River nr Warren, 43°56′N 71°52′W, 23 June 1995 [P], coll. G.W. Courtney; VERMONT: *Addison Co:* Green Mountain NF: S Br Middlebury R @ FS Rd 32 Xing, 43°56′N 72°59′W, 19 June 1991 [Pex], coll. G.W. Courtney; 22 June 1995 [P], coll. G.W. Courtney; 17 May 1996 [LP], coll. G.W. Courtney and M. Shaver; New Haven R @ Rocky Dale, 44°07′N 73°02′W, 17 May 1996 [P], coll. G.W. Courtney and M. Shaver; VIRGINIA: *Bland Co:* Wolf Creek nr Bastion, 37°10′N 81°08′W, 14 April 1999 [P], coll. G.W. Courtney; WEST VIRGINIA: *Greenbrier Co:* Greenbrier R below Renick, 37°59′N 80°21′W, 15 April 1999 [LPA], coll. G.W. Courtney; *Pocahontas Co:* Greenbrier River nr Seebert, 38°07′N 80°10′W, 8 March 1995 [L], coll. G.W. Courtney; 9 May 1995 [PA], coll. G.W. Courtney.

Etymology.—From the Latin for "bristly" (*hispidus*), in reference to the woolly appearance of the larvae.

Distribution (Fig. 175).—*Blepharicera hispida* has been collected at few sites in the central and northern Appalachians; however, these sites include a relatively broad geographic area, from Wolf Creek, Virginia, and the Greenbrier River, West Virginia, to several streams in Vermont and New Hampshire. Focused sampling effort during the winter and early spring should lead to additional records. *Blepharicera hispida* is one of the most abundant species at the South Branch Middlebury River, Wolf Creek, and Greenbrier River, whereas populations at other sites appear to be much smaller.

Bionomics.—Collection sites from the central Appalachians overlap with those of *B. gelida* and, therefore, consist primarily of larger rivers (e.g., Greenbrier River), where larvae and pupae occur in deeper riffles with moderately high current velocity (>1m/s). Data from the Greenbrier River and South Branch Middlebury River suggest that most populations are univoltine and relatively synchronous in egg hatching and development. *Blepharicera hispida* eggs apparently begin hatching in late fall and larval development is nearly completed by mid April (Greenbrier River) or mid May (New England sites). The phenology of *B. hispida* is similar to that of *B. gelida*, with both species comprising the "winter" blepharicerid fauna of the central and northern Appalachians. At central Appalachian sites, both species show broad seasonal and microhabitat overlap. *Blepharicera tenuipes* and *B. similans* also occur at most sites, but overlap only slightly with *B. hispida* (e.g., most larvae of *B. hispida* have already pupated when those of *B. tenuipes* are present and before those of *B. similans* begin hatching).

Remarks.—Larvae are similar to *B. tenuipes* but distinguished by chaetotaxy: Digitiform sensilla densely distributed over abdominal segments (*B. hispida*), rather than arranged in distinct transverse clusters (*B. tenuipes*). Pupae are indistinguishable from those of *B. coweetae* and differ only slightly from pupae of *B. tenuipes* (former two with micropunctures between abdominal papillae). As discussed earlier, adult males of several species (*B. coweetae, B. gelida, B. hispida,* and *B. coweetae*) are quite similar but can be separated by a combination of mostly genitalic characters.

Blepharicera magna Courtney, new species

(Figs. 6, 38–42, 73–74, 94, 116–123, 174)

"*Blepharicera* sp. n. #1": Johns 1996: 2 [phenology].

Diagnosis.—A large *Blepharicera*. Larva: Lateral processes on abdominal segment VII convex laterally, pointed apically; pro-

legs elongate, tapered only slightly from base to apex. Pupa: Integument of abdominal tergites shiny, without reticulate pattern but with micropunctures between papillae; abdominal papillae dark; lamellae of respiratory organ of subequal width, broadly rounded apically. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin straight, densely set with long setae; apical margin with pronounced notch near inner margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions contiguous (callis oculi absent); distal palpomere short (≈2× length of penultimate palpomere); number of parietal sensilla ≈5.

Description.—Larva (Figs. 73–74, 116–119): Measurements, instar III (N = 10): total length 5.2 mm (4.0–6.0), cranial width 0.46 mm (0.44–0.50); instar IV: fall samples (N = 10) total length 7.8 mm (6.8–8.4), cranial width 0.65 mm (0.60–0.70), antennal segments: 0.15 mm (0.13–0.18), 0.29 mm (0.28–0.30), membrane 0.07; spring samples (N = 10) total length 7.1 mm (6.4–8.0), cranial width 0.66 mm (0.62–0.70), antennal segments: 0.15 mm, 0.24 mm (0.20–0.25), membrane 0.05 (0.04–0.07). Cranial sclerites light to dark brown, without pattern; ecdysial lines with little to no stem line; posterior margin of frontoclypeal apotome extended nearly to posterior cranial margin; clypeal spines absent. Cephalothorax, trunk, lateral lobes and prolegs uniformly colored, brown to black. Anal division with posterior margin broadly rounded, the middle lobe never elongate; anal prolegs convex laterally, pointed apically. Chaetotaxy: Newly emerged (fall) larvae with pale brown setiform and taeniaform sensilla distributed generally over cephalothorax and body, and rows/clusters of digitiform sensilla medially; mature/prepupal (spring) larvae mostly glabrous but with few digitiform sensilla; both morphotypes with opaque/pale setiforms apically on prolegs; lateral lobes ventrally with numerous dark brown chaetiforms; anal division with 12–16 prominent setiforms along apex of median lobe; substernal setae digitiform, pale brown, 12–15 in number.

Pupa (Figs. 6, 94, 120–123): Measurements, male (N = 10): Total length 6.2 mm (6.0–6.5), width 3.8 mm (3.6–4.0); female (N = 10): Total length 7.3 mm (6.6–7.8), width 4.4 mm (4.2–4.6).

Cuticle dark brown; body outline broadly oval. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments; metatergite with numerous papillae medially, none laterally. Papillae dark, large, with minute spinules; gaps between papillae subequal to papilla width. Cuticle homogeneous, without reticulate pattern but with minute furrows or punctures between papillae. Branchial sclerite without papillae. Anal tergite wrinkled. Respiratory lamellae black to dark brown; middle lamellae broad, width at midpoint greater than half width of outer lamellae.

Adult male: Size: Large. Measurements (N = 5): Total length 7.7 mm (7.4–8.3), wing length 8.3 mm (8.0–8.5), width 2.4 mm (2.3–2.5).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	4.6 (4.5–4.7)	4.9 (4.8–5.1)	6.3 (6.1–6.5)
tibia	4.0 (4.0–4.1)	4.0 (4.0–4.1)	5.8 (5.6–5.9)
tarsus 1	2.2 (2.1–2.2)	1.9 (1.8–2.0)	2.1 (2.0–2.2)
2	1.0	1.0	0.8
3	0.8 (0.7–0.9)	0.7 (0.7–0.8)	0.6
4	0.5	0.5	0.4
5	0.5	0.5	0.5

Head (Fig. 39): Structure: Normal type, subholoptic. Clypeus length/width = 1.9. Eyes approximate dorsally, interocular distance approximately 0.05 mm; eye divided, dorsal division subequal in size to and well differentiated from ventral division (callis oculi absent); dorsal division with approximately 25 rows of ommatidia along midmeridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.42× head width; mandibles absent;

palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.3–1.2–2.3. Antenna with 15 articles, flagellomeres barrelshaped, broadest at middle; ultimate flagellomere 1.3× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but setose apically, f2–f12 densely setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape and base of f1 light brown, pedicel and remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (7–10), parietals (15–20), occipitals (≈20), verticals (3 or 4), postgenals (≈20).

Thorax and appendages: Tibial spurs 0–0–1; hindleg spur ≈0.3 mm; base of hind tarsomere 1 with two or three dark, spiniform sensilla. Leg-segment proportions: foreleg—34:30:16:7:6:4:4, midleg—36:30:14:7:5:4:4, hindleg—38:35:13:5:4:2:3. Chaetotaxy: Scutum mostly glabrous, but with few chaetiforms in prescutal area and several short chaetiforms posterolaterally; scutellum with diffuse cluster of 10–15 chaetiforms laterally, grading into several chaetiforms scattered medially.

Coloration: Frons and face pruinose gray, clypeus yellow. Thorax mostly dull gray-brown, pruinose. Mesoscutum brown, with yellow triangular area posteriorly; scutellum pale yellow; pleuron dark to light brown anteriorly (episternum, anterior margin of anepimeron), mostly pale posteriorly. Forecoxae dark brown; other coxae pale. Abdominal tergites dark brown, sternites light brown, pleural membrane broad, pale.

Terminalia (Figs. 41–42): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, emarginate posteriorly, with prominent U shaped depression posteromedially, densely set with setiform sensilla. Cerci well developed, slightly divergent; densely set with setiform sensilla; interlobular depression narrowly V shaped; individual cercal lobes elongate, inner margin straight, posterior margin with prominent hook near inner edge and bluntly rectangular near outer margin. Genital capsule well sclerotized, about as wide as long, posterolateral corners strongly produced. Gonostylus set with numerous setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme markedly elongate, extended beyond anterior margin of lateral parameral lobes. Parameres: Dorsal paramere pigmented laterally and apically, apex broadly rounded, medial dorsal carina weakly developed; ventral parameres longer than aedeagal rods, broad throughout, tapered to complex apex with expanded inner wall; lateral parameral lobes large, broad, outer margins emarginate.

Adult female: Size: Large. Measurements (N = 5): Total length 9.0 mm (8.5–9.3), wing length 9.9 mm (9.7–10.1), width 3.0 mm (2.8–3.1).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	5.1 (5.0–5.2)	5.2 (5.1–5.5)	7.1 (6.7–7.7)
tibia	4.1 (3.9–4.3)	4.2 (4.0–4.4)	6.2 (6.0–6.5)
tarsus 1	2.0 (2.0–2.1)	1.9 (1.8–2.0)	2.5 (2.4–2.7)
2	1.0	1.0 (0.9–1.1)	0.9 (0.8–1.0)
3	0.7 (0.6–0.8)	0.6 (0.6–0.7)	0.6 (0.5–0.7)
4	0.5	0.5 (0.4–0.5)	0.5 (0.4–0.5)
5	0.6 (0.6–0.7)	0.7 (0.6–0.7)	0.6 (0.5–0.7)

Head (Fig. 38): Structure: Normal type, subholoptic. Clypeus length/width = 2.9. Eyes approximate dorsally, interocular distance approximately 0.05 mm; eye divided, dorsal division larger than and well differentiated from ventral division (callis oculi absent laterally); dorsal division with approximately 28 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.57× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.2–1.2–1.0–2. Antenna with 15 articles, flagellomeres filiform;

ultimate flagellomere 2× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 mostly glabrous basally but with scattered setiforms apically, f2–f12 with scattered setiforms, f13 setose basally and mostly glabrous apically but terminated in several prominent setiforms; scape and base of f1 light brown, pedicel and remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (15–20), parietals (5 or 6), occipitals (≈20), verticals (5–7), postgenals (10–15).

Thorax and appendages: Tibial spurs 0–0–2; spurs asymmetrical, one each long (0.43 mm) and short (0.17 mm). Leg-segment proportions: foreleg—36:29:15:7:5:4:4, midleg—37:30:13:7:5:3:5, hindleg—39:34:14:5:3:3:3. Chaetotaxy: Scutum mostly glabrous, but with few chaetiforms in prescutal area and several short chaetiforms posterolaterally; scutellum with diffuse cluster of 10–15 chaetiforms laterally, grading into several chaetiforms scattered medially.

Coloration: Frons and face pruinose gray, clypeus yellow. Thorax mostly dull gray-brown, pruinose. Mesoscutum brown, with light brown triangular area posteriorly; scutellum yellow; pleuron dark to light brown anteriorly (episternum, anterior margin of anepimeron), mostly pale posteriorly. Forecoxae dark brown; other coxae pale. Abdominal tergites uniformly dark brown, sternites light brown, pleural membrane broad, pale.

Terminalia (Fig. 40): Posterior margin of sternite VIII broadly bilobate, medial depression poorly developed, slightly U shaped. Sternite IX (genital fork) broadly Y shaped, without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves elongate, rounded apically; inner margins of valves excavated basally, touching medially, slightly divergent apically, outer margins broadly convex. Accessory gland narrow, elongate, and extended almost to anterior margin of spermathecae basally, ovoid distally. Spermathecae 3 in number; corpora teardrop-shaped, longer than wide, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII with 6–10 setiforms laterally and few short setiforms medially; hypogynial plate pruinose; epiproct with 2 prominent setiforms apically.

Type material.—Holotype [adult male, reared]: UNITED STATES. NORTH CAROLINA: *Haywood Co:* Cataloochee Creek @ lower Xing, GSMNP 35°40′N 83°04′W, 15 May 1998, coll. G.W. Courtney, emerged 20 May. Specimen pinned, genitalia in glycerin microvial [USNM]. Allotype [adult female, reared]: same locality as holotype, 6 May 1997, emerged 15 May; pinned, genitalia in glycerin microvial [USNM]. Paratypes: same data as holotype [reared A: 2 males (EtOH), 1 male (slide), 4 males and 3 females (pinned)]; 30 April 1991 [2 male and 1 female A, reared (pinned)], coll. G.W. Courtney; 24 April 1992 [1 reared male (pinned)], coll. G.W. Courtney; 5 March 1995 [9 instar IV L (EtOH)], coll. G.W. Courtney; 26 November 1995 [10 instar IV L (EtOH)], coll. G.W. Courtney; 6 May 1997 [1 reared female (pinned)], coll. G.W. Courtney; 15 May 1998 [12 male and 6 female P (EtOH)], coll. A.J. Alverson and G.W. Courtney. Paratypes deposited in CUAC, ISU and USNM.

Other material examined.—UNITED STATES. NORTH CAROLINA: *Haywood Co:* Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W, 24 April 1992 [P]; Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W, 30 April 1991 [LP], 24–25 April 1992 [LPA], 22 May 1992 [P], 11 April 1993 [LP], 5 March 1995 [L], 7 April 1995 [LP], 30 April 1995 [P], 18–19 May 1995 [PA], 22 September 1995 [L], 21 October 1995 [L], 4 November 1995 [L], 26 November 1995 [L], 18 December 1995 [L], 5 March 1996 [L], 26 April 1996 [LP], 5 May 1996 [P], 3 October 1996 [L], 24 October 1996 [L], 19 November 1996 [L], 23

December 1996 [L], 6 May 1997 [L], 16 March 1998 [L], 15 May 1998 [PA], 12 April 1999 [L]; Palmer Ck, GSMNP, 35°38′N 83°08′W, 24 April 1992 [P]; *Swain Co:* Deep Ck, GSMNP, 35°27′N 83°26′W, 24 April 1992 [P]; Oconaluftee R, GSMNP, 35°32′N 83°17′W, 24 April 1992 [P], 24 April 1995 [L], 13 October 1995 [L], 4 November 1995 [L], 26 November 1995 [L], 18 December 1995 [L], 11 February 1996 [L], 28 February 1996 [L], 5 May 1996 [P], 3 October 1996 [L], 24 October 1996 [L], 19 November 1996 [L]; Raven Fork, GSMNP, 35°31′N 83°17′W, 24 April 1992 [P]; SOUTH CAROLINA: *Oconee Co:* Chattooga River @ Hwy 76 Xing, 34°49′N 83°18′W, 16 October 1994 [L], 6 March 1995 [P], 6 April 1995 [P], 12 May 1995 [Pex], 16 October 1995 [L], 19 October 1995 [L], 25 November 1995 [L], 9 January 1996 [L], 7 May 1996 [P], 12 May 1996 [P], 7 October 1996 [L], 31 October 1996 [L], 14 May 1998 [P], 13 April 99 [P]. Specimens from Cataloochee Ck @ lower Xing, Oconaluftee R, and Chattooga R collected by C.E. Beard, G.W. Courtney, or J.A. Johns; all other material collected by G.W. Courtney.

Etymology.—From the Latin for "large" (*magnus*), in reference to the size of this species.

Distribution (Fig. 174).—*Blepharicera magna* is confined to the southern Blue Ridge of North and South Carolina, being most abundant in streams in the southern and southeastern corner of Great Smoky Mountains National Park (e.g., Cataloochee Creek and Oconaluftee River drainages).

Bionomics.—All collection records for *B. magna* are from medium-sized (fourth- or fifth-order) streams, where larvae and pupae inhabit areas of high current velocity (>1.5 m/s). Phenological data suggest that all populations are univoltine and relatively synchronous in egg hatching and development. *Blepharicera magna* is one of four winter species in the southern Appalachians. Eggs apparently begin hatching in September and larval development is nearly completed by mid April (Johns 1996). At some sites, *B. magna* shows considerable seasonal and microhabitat overlap with *B. coweetae* and/or *B. williamsae*; however, most larval growth in *B. magna* is completed by November–December, when other winter species begin to hatch. Despite several visits to Cataloochee Creek when mature pupae were abundant, *B. magna* is one of the few species yet to be collected as adults; however, *B. magna* is among the easiest to rear, provided rocks with attached pupae are small enough to be removed from the stream (Courtney 1998).

Remarks.—*Blepharicera magna* is one of the most distinctive Appalachian species, easily recognizable as adults, pupae, and most larval instars. Because of the distinctness and large size of *B. magna*, it is surprising that the species was not discovered previously. This presumably was an artifact of *B. magna*'s relatively limited distribution and predominantly winter activity period. Although distinctive, larvae are remarkable in their seasonally dimorphic appearance. Early instars and immature (fall) fourth-instars are somewhat thin and densely set with a variety of sensilla (Figs. 73, 116–119), whereas mature/prepupal (spring) larvae are robust and essentially glabrous (Fig. 74). The latter are so strikingly different from most *Blepharicera* that they superficially resemble larval *Bibiocephala* Osten Sacken. Because of the differences between fall and spring *Blepharicera magna*, and the fact that the initial fall and spring collections were from different localities (Chattooga River and Cataloochee Creek, respectively), I had originally thought these to represent separate species. Only by examining a series of specimens from throughout the year was I able to confirm that these larval forms were, in fact, conspecifics. Pupae are equally distinctive and in some respects (body form ovoid and strongly convex) superficially resemble *Bibiocephala*. Among other Appalachian *Blepharicera*, *B. magna* is perhaps most similar to *B. gelida* but can be readily separated by the dark ab-

dominal papillae. Adult males are easily recognized by the terminalia and by the greatly enlarged dorsal eye division, the latter of which makes the male head look much like that of a female.

Blepharicera separata Alexander 1963
(Figs. 43–47, 77, 84, 126–131, 175)

Blepharicera separata Alexander 1963: 50 [original designation]; Stone 1965: 99 [catalog]; Hermann, Mullen, and Wallace 1975: 145 [suctorial discs]; Hogue 1978: 9 [synonymized with *B. capitata*].

Blepharicera capitata Loew: Hogue and Georgian 1986: 3 (in part) [taxonomic notes]; Hogue 1987: 107 (in part) [taxonomic notes]. Incorrect synonymy by Hogue 1978.

"*Blepharicera* Larva F": Hogue 1978: 30 [description, figure]; Georgian and Wallace 1983: 1237 ("type F" larvae) [collection record]; Hogue and Georgian 1986: 19 [taxonomic notes].

"*Blepharicera* sp. n. #9": Johns 1996: 2 [phenology].

Diagnosis.—A small *Blepharicera,* very similar to *B. capitata.* Larva: Stout, with prominent dorsal tubercles; body piebald, with cranial sclerites dark, remaining cephalothorax pale, abdominal segments II–V mostly dark, and anal division pale; few setiform sensilla. Pupa: Delicate, pale, with dorsomedial tubercles on abdominal segments I–VI; lamellae of respiratory organ of subequal width; abdomen with light-colored papillae evenly distributed on the dorsum. Adult male: Dorsal eye division much smaller than lower; cercus with inner margin straight, posterior margin without conspicuous lobes, outer corner obtusely rounded, not extended posteriorly as far as inner corner. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by narrow callis oculi; distal palpomere short (≈2× length of penultimate palpomere); number of parietal sensilla ≈10.

Description.—Larva (Figs. 77, 126–128): Measurements, instar I (N = 19): total length 1.0 mm (0.5–1.3), cranial width 0.16 mm (0.14–0.19); instar II (N = 75): total length 1.7 mm (1.0–2.2), cranial width 0.24 mm (0.22–0.29); instar III (N = 200): total length 2.8 mm (1.7–4.0), cranial width 0.37 mm (0.34–0.42); instar IV (N = 375): total length 3.6 mm (2.4–5.3), cranial width 0.49 mm (0.46–0.57), antennal segments 0.12 mm (0.10–0.14), 0.18 mm (0.16–0.20), membrane 0.08 mm (0.06–0.08); Larva stout, with prominent dorsal tubercles dorsomedially on each abdominal division. Cranial sclerites dark brown; ecdysial lines with abbreviated stem line; posterior margin of frontoclypeal apotome extended nearly to posterior cranial margin; clypeal spines absent. Remaining cephalothorax pale; abdominal segments II–V mostly dark, at least on trunk (prolegs sometimes pale); anal division pale. Anal division with posterior margin broadly convex, lateral processes indistinct. Chaetotaxy: Cranial sclerites with scattered digitiforms; rest of cephalothorax and body with scattered digitiforms; apex of median tubercles with stout, curved digitiforms; lateral lobes with digitiforms grading to setiforms distally; lateral lobes ventrally with few sensilla except clusters of setiforms apically; anal division with 6–8 prominent setiforms along apex of median lobe; substernal setae digitiform, yellow, 5–10 in number.

Pupa (Figs. 84, 129–131): Measurements, male (N = 30): Total length 3.8 mm (3.5–4.3), width 2.3 mm (2.1–2.7); female (N = 16): Total length 4.5 mm (4.1–4.8), width 2.7 mm (2.3–2.9). Cuticle light brown. Body roughly ovoid, somewhat dorsoventrally compressed. Integument: Dorsal papillae present, uniformly dispersed on abdominal segments; few papillae on metatergite. Papillae light in color, with no or poorly developed spinules. Cuticle between papillae glabrous, uniform in structure and pigmentation. Branchial sclerite without papillae. Anal tergite smooth, unwrinkled. Respiratory lamellae brown; middle lamellae

of respiratory organ broad basally, width at midpoint greater than half width of outer lamellae.

Adult male: Size: Small. Measurements (N = 5): Total length 3.9 mm (3.8–4.0), wing length 4.9 mm (4.7–5.2), width 1.5 mm (1.4–1.7).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	2.9 (2.7–3.0)	2.9 (2.6–3.1)	4.1 (3.8–4.3)
tibia	2.6 (2.4–2.8)	2.6 (2.4–2.7)	3.6 (3.4–3.8)
tarsus 1	1.3 (1.2–1.4)	1.3 (1.3–1.4)	1.4 (1.3–1.4)
2	0.7	0.6	0.5 (0.4–0.5)
3	0.5 (0.4–0.5)	0.5 (0.4–0.5)	0.3
4	0.2 (0.2–0.3)	0.2	0.2
5	0.3	0.3	0.3

Head (Fig. 44): Structure: Normal type, dichoptic. Clypeus length/width = 2.2. Eyes well separated dorsally, interocular distance approximately 0.11 mm; eye divided, dorsal division much smaller than and contiguous with ventral division (callis oculi absent); dorsal division with approximately 12 rows of ommatidia along midmeridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.40× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.4–1.4–3.9. Antenna with 15 articles, flagellomeres somewhat barrel-shaped basally, cylindrical distally; ultimate flagellomere 1.1× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 glabrous basally but densely setose apically, f2–f12 setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape and base of f1 pale, pedicel and remaining flagellomeres concolorous, light brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (5–10), parietals (0), occipitals (≈20), verticals (2 or 3), postgenals (≈5).

Thorax and appendages: Tibial spurs 0–0–1; hindleg spur ≈0.12 mm; base of hind tarsomere 1 with two or three dark, spiniform sensilla. Leg-segment proportions: foreleg—34:31:15:8:6:2:4, midleg—35:31:15:7:6:2:4, hindleg—39:35:13:5:3:2:3. Chaetotaxy: Scutum mostly glabrous, but with few scattered chaetiforms in prescutal area; scutellum with cluster of ≈15 chaetiforms laterally and few scattered chaetiforms medially.

Coloration: Frons and face mostly light brown to gray, clypeus pale. Thorax mostly light brown, pruinose. Mesoscutum and scutellum light brown; pleuron light brown anteriorly (episternum, anterior margin of anepimeron), mostly pale posteriorly. Coxae pale. Abdominal tergites and sternites light brown, pleural membrane broad, pale.

Terminalia (Figs. 46–47): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, deeply emarginate posteromedially, set with setiform sensilla. Cerci well developed, parallel; set with setiform sensilla; interlobular depression U shaped; individual cercal lobes longer than broad, inner margin straight, posterior margin without conspicuous lobes or processes but outer corner obtusely rounded, not extended posteriorly as far as inner corner. Genital capsule well sclerotized, slightly longer than wide, posterolateral corners strongly produced. Gonostylus set with numerous setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme markedly elongate, extended nearly to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere lightly pigmented laterally and apically, apex weakly incised or entire on either side of weak medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, tapered to simple apex with elongate inner wall; lateral parameral lobes large, broad, outer margins straight, divergent.

Adult female: Size: Small. Measurements (N = 3): Total length 4.8 mm (4.5–5.0),

wing length 5.0 mm (4.9–5.2), width 1.8 mm (1.7–1.8).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	3.0 (3.0–3.1)	3.0 (3.0–3.1)	3.9
tibia	2.6	2.6	3.2 (3.1–3.3)
tarsus 1	1.2	1.3	1.4
2	0.6	0.6	0.7
3	0.4	0.4	0.5
4	0.2	0.2	0.2
5	0.3	0.3	0.3

Head (Fig. 43): Structure: Normal type, subholoptic. Clypeus length/width = 2.2. Eyes approximate dorsally, interocular distance approximately 0.03 mm; eye divided, dorsal division subequal in size to and nearly contiguous with ventral division (callis oculi narrow); dorsal division with approximately 15 rows of ommatidia along midmeridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.36× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.2–1.2–2.6. Antenna with 15 articles, flagellomeres cylindrical; ultimate flagellomere 2× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–13 sparsely set with setiforms, f13 terminated in several prominent setiforms; scape, pedicel, and base of f1 pale, remaining flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (15–20), parietals (≈10), occipitals (10–15), verticals (3 or 4), postgenals (≈5).

Thorax and appendages: Tibial spurs 0–0–2; spurs asymmetrical, one each long (0.15 mm) and short (0.06 mm). Leg-segment proportions: foreleg—36:31:14:7:5:2:4, midleg—36:31:15:7:5:3:4, hindleg—38:31:14:7:5:2:3. Chaetotaxy: Scutum mostly glabrous; scutellum with cluster of ≈10 chaetiforms laterally and few scattered chaetiforms medially.

Coloration: Frons, face, and clypeus brown to light brown. Thorax mostly light brown, pruinose. Mesoscutum brown to light brown, except pale posteriorly; scutellum light brown; pleuron brown anteriorly (episternum, anterior margin of anepimeron), mostly pale posteriorly. Forecoxae light brown; other coxae pale. Abdominal tergites brown, sternites light brown, pleural membrane broad, pale.

Terminalia (Fig. 45): Posterior margin of sternite VIII broadly bilobate, medial depression well developed, broadly U shaped. Sternite IX (genital fork) broadly V shaped, without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves elongate, subrectangular, truncate apically; inner margins of valves excavated slightly near base, slightly divergent apically, outer margins slightly convex. Accessory gland with short base, ovoid distally, extended to anterior margin of spermathecae. Spermathecae 3 in number; corpora pearshaped, longer than wide, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII without setiforms; hypogynial plate mostly glabrous, valves pruinose; epiproct with 2 prominent setiforms apically.

Type material.—Holotype [male]: UNITED STATES. MAINE: *Somerset Co:* Bingham, along the Kennebec River, 17 July 1937, coll. C.P. Alexander [USNM].

Material examined.—CANADA. NEW BRUNSWICK: *Charlotte Co:* Saint Stephen, 27 June 1965 [LP]; *Northumberland Co:* Boiestown, 13 July 1931 [A]; *York Co:* Nashwaak R below Stanley, 46°16′N 66°40′W, 1 June 1998 [LP]; UNITED STATES. ALABAMA: *Blount Co:* Hendrick Mill Br, 33°52′N 86°33′W, 15–20 April 1990 [A]; GEORGIA: *Lumpkin Co:* Hightower R, 11 April 1941 [L]; *Towns Co:* Hiawassee, 16 June 1945 [A]; MAINE: *Somerset Co:* E branch Wesserunset Stream @ Athens, 44°55′N 69°40′W, 6 June 1987 [LP]; Pleasant Pond Stream @ Caratank, 45°14′N 69°59′W, 24 June 1966 [L]; *Washington Co.* Narraguagus R @ Hwy 9, 44°50′N

68°04′W, 5 June 1987 [L], 7 June 1998 [LPA]; NEW HAMPSHIRE: *Grafton Co:* Franconia, 44°13′N 71°44′W [A]; NEW YORK: *Essex Co:* Schroon R @ Sharp Bridge CG, 44°02′N 73°40′W, 17 June 1991 [Pex]; NORTH CAROLINA: *Alleghany Co:* Little R @ Sparta, 36°29′N 81°06′W, 24 May 1995 [LP]; *Avery Co:* Linville R @ Linville Falls CG, 35°57′N 81°57′W, 22 May 1970 [L]; *Clay Co:* Hiwasee River, 35°03′N 83°53′W, 20 May 1995 [LP]; *Haywood Co:* Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W, 18 May 1995 [LP], 19 June 1996 [L], 15 May 1998 [L]; *Henderson Co:* Mills R nr Pisgah boundary, 35°23′N 82°35′W, 25 May 1995 [L]; *Macon Co:* lower Dryman Fork, 35°02′N 83°24′W, 2 May 1991 [L], 24 April 1992 [L], 29 March 1995 [L], 18 May 1995 [LP], 23 May 1995 [LPA], 3 June 1995 [LP], 8 May 1996 [L], 15 May 1998 [LP]; lower Shope Fork, CHL, 35°03′N 83°26′W, 29 March 95 [L]; *Madison Co:* Spring Ck @ Rocky Bluff, 35°51′N 82°50′W, 29 April 1991 [L]; *McDowell Co:* Mill Ck @ Old Fort, 35°37′N 82°10′W, 3 May 1991 [L]; North Fork Catawba River, 35°48′N 82°01′W, 3 May 1991 [LP]; *Swain Co:* Deep Ck, GSMNP, 35°27′N 83°26′W, 21 May 1970 [L]; Noland Ck, GSMNP, 35°27′N 83°31′W, 24 May 1974 [L]; Oconaluftee R, GSMNP, 35°32′N 83°17′W, 18 May 1995 [L], 4 June 1995 [LPA], 3 June 1996 [L]; SOUTH CAROLINA: *Oconee Co:* Brasstown Ck above falls, 34°43′N 83°18′W, 27 April 1994 [L], 17 May 1995 [LP], 7 May 1997 [LP]; Chattooga R @ Hwy 76, 34°49′N 83°18′W, 2 May 1991 [LP], 23 May 1992 [LPA], 26 April 1994 [L], 24 May 1994 [LP], 21 April 1995 [L], 12–19 May 1995 [LPA], 7 May 1996 [L], 12 May 1996 [L], 2 June 1996 [P], 7 May 1997 [LP], 14 May 1998 [LP]; *Pickens Co:* Rocky Bottom Ck @ Rt 178, 35°02′N 82°48′W, 16 May 1994 [LP]; TENNESSEE: *Polk Co:* Parksville, 35°05′N 84°39′W, 25 April 1938 [L—identification tentative]; VERMONT: *Bennington Co:* Roaring Bk @ Chiselville, 43°04′N 73°07′W, 24 June 1995 [LP]; *Windsor Co:* White R 3mi above Bethel, 43°47′N 72°39′W, 19 June 1991 [LP], 23 June 1995 [LPA], 30 May 1998 [L]; VIRGINIA: *Bath Co:* Ck @ Blowing Springs Recreational Area, 38°04′N 79°53′W, 18 April 1968 [L]; *Montgomery Co:* Little R nr Snowville, 37°02′N 80°33′W, 26 May 1995 [LP]; *Washington Co:* S Fk Holston River, 36°39′N 81°50′W, 4 May 1991 [L]; Straight Creek, Mt Rogers, 36°38′N 81°43′W, 4 May 1991 [L]; WEST VIRGINIA: *Greenbrier Co:* Greenbrier R below Renick, 37°59′N 80°21′W, 15 April 1999 [L]; *Pocahontas Co:* Greenbrier R @ Seebert, 38°07′N 80°10′W, 9 May 1995 [PA].

Distribution (Fig. 175).—*Blepharicera separata* is one of the most widespread Appalachian species, ranging from northern Alabama, South Carolina, and Georgia to maritime Canada. Although locally abundant at several sites, most collections include few individuals.

Bionomics.—In the northern part of its range, *B. separata* occurs primarily in larger rivers, whereas southern records include both large rivers and mid-sized streams. At some sites, larval abundance can be relatively high (e.g., >200/m^2 [Johns 1996]). As with its presumed close relative *B. capitata,* most collections are from habitats with relatively low current velocity (<1 m/s). In areas of higher current velocity, larvae and pupae typically occur on the protected lateral margins of rocks. Collection records from the southern Appalachians indicate that *B. separata* is active primarily during late spring and early summer. Northern populations appear to be active primarily during the summer. Phenological data from several areas suggest that most populations are univoltine and exhibit relatively synchronous egg hatching and development. Based on collections from several human-impacted streams, this species is apparently somewhat more tolerant of environmental degradation (e.g., sedimentation) than most *Blepharicera.*

Remarks.—As discussed earlier (see *B. capitata*), *B. separata* is difficult to distin-

guish from *B. capitata*, and both species are presumed to be closely related. The larvae of both are distinct in the possession of prominent tubercles dorsomedially on each body division. *Blepharicera separata* has a characteristic piebald coloration, which, in combination with dorsal tubercles, makes even first-instar larvae recognizable. Slight variations in the piebald pattern are evident: e.g., in most populations, the dorsum of abdominal segments II–V is dark medially and laterally onto the proleg (Fig. 77); however, in Greenbrier River (WV) populations, the dark area is confined to a well-delineated patch surrounding and including the dorsal tubercle. Similar coloration is typical of certain populations of *B. ostensackeni* Kellogg, a species from western North America (personal observations). Adult *B. separata* and *B. capitata* are very similar, which accounts for their synonymy by Hogue (1978). Females can be separated only by dissection and clearing of the terminalia, which permits viewing of the distinctive spermathecal ducts of *B. capitata*. Males are somewhat easier to distinguish, in that dissection is not necessary; however, the angle by which cerci are viewed is critical to accurate identification. The latter can influence whether or not the inner cercal margin appears expanded, a characteristic of *B. capitata*. I have found that the shape of the posterior cercal margin is less dependent on viewing angle and, thus, a better taxonomic feature. In this character, the two species are quite distinct: *B. capitata* with lobelike outer margin (Fig. 65), *B. separata* with obtuse outer margin (Fig. 46).

Blepharicera similans Johannsen 1929
(Figs. 67–68, 70, 132–139, 175)

Blepharocera similans Johannsen 1929: 123 [original designation], 1934: 50 [taxonomic notes]; Alexander 1953: 45 [taxonomic notes], 1958: 820 [species list], 1963: 45 [redescription, keys].

Blepharicera similans Johannsen: Stone 1965:99 [catalog]; Hogue 1978: 16 [redescription, adult keys, figures]; Carlson 1981: 68 [as bioindicators]; Hogue and Georgian 1986: 16 [taxonomic notes, keys, figures]; Hogue 1987: 120 [redescription, keys, figures]; Johns 1996: 2 [phenology]; Courtney 1998: 743 [rearing technique]; Courtney and Duffield 2000: 87 [in trout diets].

"*B. similans* (Johannsen)": Georgian and Wallace 1983: 1237 [collection records].

"*Blepharoceridae*": Amos 1977: 576 [general natural history, figures].

"*Blepharicera* Larva B": Hogue 1978: 27 [description, collection records].

Diagnosis.—A small *Blepharicera*. Larva: Dorsal secondary sensilla mostly globose; body usually uniformly colored, pale; ecdysial stem line long basally, frontoclypeal apotome separated from posterior margin of cranium and noticeably darker than rest of head. Pupa: Middle lamellae of respiratory organ narrow basally, width approximately half width of outer lamellae; integument of abdominal tergites with minute, dark papillae bearing microscopic spinules apically. Adult male: Dorsal eye division much smaller than lower; cercus with inner margin shallowly convex and expanded slightly near base, apical margin straight with obtuse angulate outer margin; median aedeagal filament distinctly longer than lateral filaments. Adult female: 2 spermathecae with uniformly sclerotized and unpigmented ducts; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla ≈ 25.

Description.—See Hogue (1987).

Type material.—Holotype [male]: UNITED STATES. MASSACHUSETTS: *Hampshire Co:* Orient Springs, near Amherst, 25 June 1927, coll. C.P. Alexander [CUI].

Collection localities [see Hogue (1978) for additional sites].—CANADA. QUEBEC: *Réserve Faunique du Saint-Maurice:* Aubin Ck; Boitel Ck; Rivièrre Matawin. UNITED STATES. GEORGIA: *Rabun Co:* Addie Branch @ FS Rd 86, 34°58′N

83°15′W; Holcomb Ck @ FS Rd 7, 34°58′N 83°16′W; Tottery Pole Ck, 34°57′N 83°13′W; West Fork Chattooga River, 34°57′N 83°12′W; *Towns Co:* Tallulah R nr Tate Branch, 34°57′N 83°33′W; MAINE: *Somerset Co:* E branch Wesserunset Stream, 44°55′N 69°40′W; MASSACHUSETTS: *Berkshire Co:* Cold R along Hwy 2, 42°38′N 72°58′W; NEW HAMPSHIRE: *Carroll Co:* Swift R bel. covered bridge, 44°00′N 71°14′W; *Coos Co:* Wild River @ FS Rd 12, 44°19′N 71°01′W; Zealand River @ Sugarloaf Trail, 44°15′N 71°30′W; NEW YORK: *Essex Co:* Owen Pond Bk nr W Ausable, 44°19′N 73°54′W; Schroon R @ Sharp Bridge CG, 44°02′N 73°40′W; Grove Bk @ Hwy 22 // 9N, 44°00′N 73°27′W; Styles Brook @ Hwy 9N, 44°17′N 73°47′W; W Ausable R nr Owen Pond, 44°19′N 73°54′W; NORTH CAROLINA: *Alleghany Co:* Little R @ Sparta, 36°29′N 81°06′W; *Clay Co:* Big Tuni Ck 1mi above Tusquitee R, 35°06′N 83°41′W; Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W; Buck Ck nr confl Park Ck, 35°03′N 83°35′W; Fires Ck @ FS Rd 340A, 35°06′N 83°50′W; Hiwasee River, 35°03′N 83°53′W; Leatherwood Falls, 35°05′N 83°51′W; Park Ck nr confl Buck Ck, 35°03′N 83°35′W; Rock House Ck nr Fires Ck, 35°06′N 83°50′W; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W; Cataloochee Ck, GSMNP, 35°40′N 83°04′W; W Fk Pigeon R @ "falls", 35°20′N 82°54′W; W Fk Pigeon R @ Hwy 215, 35°22′N 82°55′W; W Fk Pigeon R @ Sunburst, 35°22′N 82°56′W; *Henderson Co:* Mills R nr Pisgah boundary, 35°23′N 82°35′W; *Macon Co:* Bearpen Ck @ Rd 67, 35°02′N 83°30′W; Big Buck Ck @ Hwy 64, 35°07′N 83°16′W; Cullasaja R nr Goldmine Rd, 35°05′N 83°15′W; Hemp Patch Ck @ FS Rd 67, 35°01′N 83°30′W; Hurricane Ck @ FS Rd 67, 35°03′N 83°30′W; Jarrett Ck @ Rd 437, 35°09′N 83°37′W; lower Ball Ck, CHL, 35°03′N 83°26′W; lower Dryman Fork, 35°02′N 83°24′W; lower Shope Fork, CHL, 35°03′N 83°26′W; Nantahala River nr Curtis Ck, 35°04′N 83°31′W; Shope Fk @ Rd 7276, CHL, 35°03′N 83°27′W; small Ck below Wayah Crest, 35°09′N 83°34′W; Wayah Ck nr Rd 388, 35°09′N 83°32′W; *Madison Co:* Spring Ck @ Rocky Bluff, 35°51′N 82°50′W; *McDowell Co:* Curtis Ck near CG, 35°41′N 82°11′W; Mill Ck @ Old Fort, 35°37′N 82°10′W; North Fork Catawba River, 35°48′N 82°01′W; *Swain Co:* Beech Flats Prong, Oconaluftee R, GSMNP, 35°38′N 83°22′W; Oconaluftee R, GSMNP, 35°32′N 83°17′W; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W; N Fk French Broad R, 35°13′N 82°51′W; PENNSYLVANIA: *Pike Co:* Big Bushkill Ck, DWG, 41°05′N 75°00′W; Dingmans Ck, DWG, 41°13′N 74°53′W; Little Bushkill Ck, DWG, 41°05′N 75°00′W; Raymondskill Ck, DWG, 41°17′N 74°50′W; SOUTH CAROLINA: *Oconee Co:* Brasstown Ck above falls, 34°43′N 83°18′W; Chattooga R @ Hwy 76, 34°49′N 83°18′W; *Pickens Co:* Green Ck, Table Rock trail, 35°02′N 82°42′W; TENNESSEE: *Cocke Co:* Cosby Ck, GSMNP, 35°45′N 83°12′W; trib Cosby Ck, GSMNP, 35°46′N 83°13′W; *Johnson Co:* Beaverdam Ck @ Backbone, 36°35′N 81°49′W; Fagall Branch, 36°34′N 81°51′W; *Sevier Co:* Little Pigeon R, GSMNP, 35°44′N 83°24′W; M Prong nr lower Xing, GSMNP, 35°42′N 83°21′W; Ramsey Prong nr Cascades Trail, GSMNP, 35°42′N 83°19′W; Porters Ck @ trailhead, GSMNP, 35°41′N 83°23′W; Porters Ck above Little Pigeon R, GSMNP, 35°42′N 83°22′W; Injun Ck nr Greenbrier, GSMNP, 35°43′N 83°24′W; trib Little Pigeon River, GSMNP, 34°57′N 83°12′W; W Prong @ Chimney, GSMNP, 35°38′N 83°29′W; VERMONT: *Addison Co:* Middlebury R bel. Ripton, 43°58′N 73°02′W; New Haven R @ Rocky Dale, 44°07′N 73°02′W; New Haven R below NH Mills, 44°05′N 73°06′W; S Br Middlebury River, 43°57′N 73°01′W; Texas Falls (Hancock Br), 43°56′N 72°53′W; *Bennington Co:* Metawee R @ Hwy 30, 43°16′N 73°07′W; Roaring Bk @ Chiselville, 43°04′N 73°07′W; Roaring Bk @ FS Rd FH-6, 43°02′′N 73°05′W; *Rutland Co:* Black Bk @ FS Rd 10, 43°22′′N 72°57′W;

Flower Brook @ Hwy 133, 43°32′N 73°03′W; Furnace Bk below hatchery, 43°45′′N 72°58′W; Mendon Brook nr Mendon, 43°39′′N 72°55′W; Poultney River, 43°30′N 73°10′W; Ten Kilns Bk @ FS Rd 10, 43°21′N 72°54′W; *Windham Co:* Wardsboro Bk nr West R, 43°04′N 72°44′W; West R nr Wardsboro Bk, 43°04′N 72°44′W; *Windsor Co:* Brandon Bk nr CG entrance, 43°51′′N 72°53′W; Greendale Bk @ CG, 43°21′N 72°49′W; White R 3mi above Bethel, 43°47′N 72°39′W; VIRGINIA: *Botetourt Co:* Jennings Ck @ Hwy 614, 37°32′N 79°37′W; *Giles Co:* Stoney Ck nr White Rocks, 37°26′N 80°31′W; White Rocks Branch, 37°26′N 80°30′W; *Montgomery Co:* Little R nr Snowville, 37°02′N 80°33′W; *Washington Co:* S Fk Holston River, 36°39′N 81°50′W; Straight Creek, Mt Rogers, 36°38′N 81°43′W; WEST VIRGINIA: *Fayette Co:* Cathedral Falls nr Gauley Bridge, 38°09′N 81°11′W.

Distribution (Fig. 175).—*Blepharicera similans* is one of the most widespread and abundant blephariceridsin eastern North America, second only to *B. tenuipes* in its range. *Blepharicera similans* shows an exceptional latitudinal range, extending from the southern Appalachians (northern Georgia and South Carolina) to maritime Canada.

Bionomics.—In terms of habitat, *B. similans* is perhaps the most variable Appalachian species. In the southern part of its range, the species ranges from headwater trickles and waterfalls to large rivers. Northern populations are less variable, being restricted primarily to large and mid-sized rivers. At many sites, especially during the summer, *B. similans* can occur in remarkably high densities (>500 larvae/m^2 [unpublished data]). Larval microhabitat can be equally variable, including a wide range of current velocities (0.5 to >2 m/s). *Blepharicera similans* is clearly a summer species (Johns 1996) but with a greatly protracted activity period. In some southern populations, larvae are present from late spring to mid fall. Phenological data from these and other areas suggest that many populations are either multivoltine or exhibit highly asynchronous egg hatching and development.

Remarks.—Based partly on the broad distribution, wide range of stream types, and highly variable microhabitats, *B. similans* is a prime candidate for the presence of sibling species. Attempts to address this issue using cytological information have proved difficult. In samples analyzed thus far, the polytene chromosomes of *B. similans* have been poorly developed and difficult to compare across populations and between species whose chromosomes have provided good preparations (e.g., *B. williamsae*). In other morphological features, *B. similans* is relatively easy to differentiate from other Appalachian species: based on the larval chaetotaxy (globose sensilla), pupal respiratory organ (middle lamellae narrow basally) and microsculpture (dark papillae and glabrous background), and adult terminalia (cercal shape of male and atrophied median spermatheca of female). Exceptions include some populations in the southern Appalachians (e.g., Chattooga River), where larval chaetotaxic differences become somewhat less reliable (i.e., *B. similans* and *B. cherokea* difficult to separate), and pupal differences are obscured in at least one stream (*B. similans* and *B. chattooga* [endemic to Chattooga River] indistinguishable).

Blepharicera tenuipes (Walker) 1848
(Figs. 57, 63, 90, 166–168, 176)

Asindulum tenuipes Walker 1848: 86 [original designation]; Osten Sacken 1878a: 17 [incorrectly synonymized with *B. capitata*].

Blepharocera capitata Loew: Osten Sacken 1878a: 17 (in part) [catalog], 1878b: 405 (in part) [historical and taxonomic notes, adult keys], 1891: 408 (in part) [review of family, adult keys], 1895: 150 (in part) [historical and taxonomic notes, adult keys]; Comstock and Comstock 1895:

432 [misidentification]; Kellogg 1900a: 41 [misidentification], 1900b: 305 [misidentification], 1903: 197 (in part) [general descriptions, ecology].

Blepharocera tenuipes (Walker): Aldrich 1905: 172 (in part) [catalog]; Riley 1906: 297 [eye morphology]; Kellogg 1907: 12 (in part) [review of Nearctic fauna, adult keys], Kellogg 1908: 152 (in part) [review of Nearctic fauna, adult keys]; Curran 1923: 268 [distributional notes]; Johannsen 1934: 54 [brief description of larva and pupa, figures]; Hennig 1952: 38 [larval morphology]; Alexander 1953: 44 (in part) [taxonomic notes], 1958: 820 (in part) [species list], 1963: 51 (in part) [redescription, keys].

Blepharicera tenuipes (Walker): Stone 1965:99 [catalog]; Hogue 1978: 19 (in part) [redescription, keys, figures], 1981: 195 [figure of wing]; Carlson 1981: 68 [as bioindicators]; Hogue and Georgian 1986: 16 [taxonomic notes, keys]; Hogue 1987: 123 [redescription, keys, figures]; Courtney 1998: 745 [rearing technique].

Blepharicera tenuipes Walker: Walley 1927: 113 (in part) [taxonomic notes].

Blepharicera capitata Loew: Cole 1969: 64 (after Kellogg) [figure].

"*Blepharicera* Larva A": Hogue 1978: 27 [description, records, figure].

Diagnosis.—A medium-sized *Blepharicera*. Larva: Dorsal secondary sensilla mostly fusiforms, arranged in two broad, transverse bands medially; color variable but usually uniformly light to dark brown. Pupa: Ovoid in shape; integument of abdominal tergites glabrous; papillae dark, uniformly spaced, with few/no furrows between papillae; lamellae of respiratory organ of subequal width, broadly rounded apically. Adult male: Dorsal eye division much smaller than lower; cercus with inner margin straight, posterior margin with pointed lobe near medial margin; apex of dorsal paramere deeply incised on either side of medial dorsal carina. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla >30.

Description.—See Hogue (1987).

Type material.—Holotype [female]: CANADA. ONTARIO: Albany River [BMNH].

Collection localities [see Hogue (1978) for additional sites].—CANADA. NEW BRUNSWICK: *Carleton Co:* Miramichi R along Rt 107, 46°30′N 67°06′W; *York Co:* Nashwaak R below Stanley, 46°16′N 66°40′W; *Albert Co:* Cleveland Bk, Fundy NP; NEWFOUNDLAND: Dunn's River, Burin Peninsula; QUEBEC: *Réserve Faunique du Saint-Maurice:* Aubin Ck; Boitel Ck; Rivière Matawin. UNITED STATES: MAINE: *Oxford Co:* Wild R @ Hastings, 44°21′N 70°58′W; *Somerset Co:* E branch Wesserunset Stream, 44°55′N 69°40′W; Gulf Stream, 45°05′N 69°48′W; *Washington Co:* Narraguagus R @ Hwy 9, 44°50′N 68°04′W; MICHIGAN: *Baraga Co:* Perch R @ Hwy 28, 46°31′N 88°39′W; Sturgeon R nr CG, 46°34′N 88°39′W; *Gogebic Co:* Black R nr Potawatomi Falls, 46°38′N 90°03′W; Presque Isle R @ S boundary Rd, 46°41′N 89°58′W; *Ontanagon Co:* Blowdown Ck nr L Carp R, 46°43′N 89°49′W; E Br Ontanagon R @ CG, 46°30′N 88°56′W; Little Carp R nr Greenstone, 46°43′N 89°49′W; NEW HAMPSHIRE: *Carroll Co:* Chocorua R @ Hwy 16, 43°55′N 71°13′W; Saco R above Sawyer Rock, 44°04′N 71°19′W; Swift R above lower falls, 44°00′N 71°15′W; Swift R bel. covered bridge, 44°00′N 71°14′W; *Coos Co:* Ammonoosuc R @ FS Rd 4, 44°16′N 71°22′W; Ammonoosuc R nr Halfway, 44°15′N 71°24′W; Jefferson Bk @ upper Xing, 44°17′N 71°21′W; Little Bear Bk @ FS Rd 4, 44°19′N 71°22′W; S Br Israel R @ FS Rd 4, 44°19′N 71°22′W; Wild River @ FS Rd 12, 44°19′N 71°01′W; Zealand River @ Sugarloaf Trail, 44°15′N 71°30′W; *Grafton Co:* Baker River nr Warren, 43°56′N 71°52′W; Drake Brook @ Hwy 49,

43°56′N 71°30′W; East Pond Bk @ FS Rd 30, 43°59′N 71°35′W; falls above Sugar Hill Overlook, 44°00′N 71°25′W; N Br Gale R @ FS Rd 92, 44°14′N 71°36′W; Sawyer R @ Hwy 302, 44°05′N 71°20′W; Sawyer R nr Signal Ridge, 44°04′N 71°23′W; Scarface Brook @ FS Rd 92, 44°13′N 71°38′W; Walker Bk, Franconia Notch, 44°08′N 71°40′W; Wild Ammonoosuc River, 44°05′N 71°51′W; NEW YORK: *Essex Co:* N Fk Boquet R @ Hwy 73, 44°06′N 73°42′W; S Fk Boquet R @ Hwy 73, 44°06′N 73°41′W; Schroon R @ Sharp Bridge CG, 44°02′N 73°40′W; Grove Bk @ Hwy 22 // 9N, 44°00′N 73°27′W; Styles Brook @ Hwy 9N, 44°17′N 73°47′W; *Hamilton Co:* Bear Bk @ Hwy 28 Xing, 43°50′N 74°32′W; PENNSYLVANIA: *Monroe Co:* Bushkill Ck (?) @ Ressaca, 41°06′N 75°05′W; *Pike Co:* Little Bushkill Ck, DWG, 41°05′N 75°00′W; VERMONT: *Addison Co:* Middlebury R bel. Ripton, 43°58′N 73°02′W; Moss Glen Falls, 44°01′N 72°50′W; New Haven R @ Rocky Dale, 44°07′N 73°02′W; New Haven R below NH Mills, 44°05′N 73°06′W; S Br Middlebury River, 43°57′N 73°01′W; Brandy Ck @ FS Rd 59, 43°57′N 72°58′W; Sparks Brook @ FS Rd 54, 44°00′N 72°58′W; Texas Falls (Hancock Br), 43°56′N 72°53′W; trib Austin Bk, 44°03′N 72°51′W; *Bennington Co:* Metawee R @ Hwy 30, 43°16′N 73°07′W; Roaring Bk @ Chiselville, 43°04′N 73°07′W; Roaring Bk @ FS Rd FH-6, 43°02′′N 73°05′W; Roaring Bk nr confl S Fk, 43°02′′N 73°06′W; *Rutland Co:* Flower Brook @ Hwy 133, 43°32′N 73°03′W; Furnace Bk below hatchery, 43°45′′N 72°58′W; Mendon Brook nr Mendon, 43°39′′N 72°55′W; Poultney River, 43°30′N 73°10′W; Ten Kilns Bk @ FS Rd 10, 43°21′N 72°54′W; *Washington Co:* upper Mad R @ Hwy 100, 44°10′N 72°49′W; *Windsor Co:* Brandon Bk nr CG entrance, 43°51′′N 72°53′W; Greendale Bk @ CG, 43°21′N 72°49′W; White R 3mi above Bethel, 43°47′N 72°39′W; VIRGINIA: *Bland Co:* Wolf Ck nr Bastion, 37°10′N 81°08′W; *Giles Co:* Stoney Ck nr White Rocks, 37°26′N 80°31′W; *Montgomery Co:* Little R nr Snowville, 37°02′N 80°33′W; WEST VIRGINIA: *Fayette Co:* Cathedral Falls nr Gauley Bridge, 38°09′N 81°11′W; *Greenbrier Co.:* Greenbrier R below Renick, 37°59′N 80°21′W; *Nicholas Co:* Cherry R @ Fenwick, 38°13′N 80°35′W; Gauley R nr Cherry R, 38°17′N 80°38′W; *Pocahontas Co:* Greenbrier R @ Seebert, 38°07′N 80°10′W; *Raleigh Co:* Kates Branch (Long Bottom, New River), 37°43′N 80°55′W; WISCONSIN: *Ashland Co:* Brunsweiler R @ Co Rd C, 46°24′N 90°48′W; *Bayfield Co:* Marengo Ck @ Rd 384, 46°19′N 91°00′W; *Douglas Co:* Brule R nr CG, 46°36′N 91°34′W; *Iron Co:* Montreal R @ Hwy 2, 46°29′N 90°16′W.

Distribution (Fig. 176).—*Blepharicera tenuipes* is the most widespread blepharicerid in eastern North America, ranging from the central Appalachians to maritime Canada (including Newfoundland), and west to James Bay and the Great Lakes Region. It is the only blepharicerid found in the latter area.

Bionomics.—*Blepharicera tenuipes* occurs in a wide range of sites but is most abundant in small- to medium-sized streams. The immature stages typically occur in areas of moderately high current velocity (>1 m/s). Phenological data suggest that most populations are univoltine but relatively asynchronous in egg hatching and development. At many sites, this species and *B. similans* are sympatric but somewhat isolated temporally, with *B. tenuipes* active earlier in the year. Perhaps because of its early description (1848) and wide distribution in areas frequented by dipterists, most early accounts of *Blepharicera* biology pertain to this species (e.g., Johannsen 1903, 1934; Kellogg 1900a, b [as *B. capitata*], 1907).

Remarks.—As in *B. similans*, the widespread distribution and broad range of stream types suggest that *B. tenuipes* is another candidate for sibling speciation. Also, as in the former species, preparations of polytene chromosomes have been poor,

making comparisons within and between species difficult. Throughout much of its range, *B. tenuipes* is sympatric with only *B. similans,* which makes recognition of larvae, pupae, and adults relatively easy. Problematic sites include those with *B. hispida,* a species very similar to *B. tenuipes.* Larvae of these species can be distinguished by chaetotaxy (cf. Figs. 109, 110–112), pupae by subtle differences in microsculpture (cf. Figs. 113–115 and Figs. 166–168), and adult males by relative development of the dorsal eye division (larger in *B. hispida*). As in most eastern *Blepharicera,* adult females are nearly indistinguishable. *Blepharicera tenuipes* also shares many similarities with the allopatric species, *B. coweetae.*

Blepharicera tuberosa Courtney, new species

(Figs. 15–17, 48–52, 140–145, 174)

"*Blepharicera* sp. n. #2": Johns 1996: 2 [phenology].

Diagnosis.—A small to medium-sized *Blepharicera.* Larva: Prominent tubercles along each side of dorsal midline; dorsal sensilla mostly fusiforms, arranged in broad, transverse bands medially; body color usually uniformly light to dark brown. Pupa: Middle lamellae of respiratory organ narrow basally, width approximately half width of outer lamellae; integument of abdominal tergites set with poorly developed papillae but with circular patches of spinules, each having appearance of light-colored papilla or papilla surrounded by light-colored halo; integument with numerous micropunctures between spinule patches. Adult male: Dorsal eye division much smaller than lower; cercus narrow, elongate, inner margin straight, acutely pointed apically. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions separated by broad callis oculi; distal palpomere elongate (≈3× length of penultimate palpomere); number of parietal sensilla <10.

Description.—Larva (Figs. 15–16, 140–142): Measurements, instar III (N = 4): total length 3.8 mm (3.5–4.3), cranial width 0.43 mm (0.40–0.44); instar IV: (N = 15) total length 5.8 mm (4.3–6.8), cranial width 0.56 mm (0.54–0.58), antennal segments 0.14 mm (0.13–0.15), 0.22 (0.18–0.25), membrane 0.03 mm (0.0–0.05). Cranial sclerites mostly brown to dark brown; posterodorsal region of genae and posterior half of frontoclypeal apotome dark and area medial to eyespots pale; in some individuals, frontoclypeal apotome pale anteriorly; ecdysial lines with short stem line; posterior margin of frontoclypeal apotome separated from posterior cranial margin; clypeal spines absent. Trunk uniformly brown to cream-colored; tubercles somewhat darker than background color. Anal division with posterior margin truncate; anal prolegs moderately developed, triangular. Chaetotaxy: Cranial sclerites largely glabrous, with few short fusiforms, and rows of setiforms near labral margin; cephalothorax with scattered, short fusiforms; trunk mostly glabrous dorsally, except for dorsal tubercles, which are densely set with stout fusiforms and 1 elongate setiform; base of lateral lobes with scattered setiforms, grading to more numerous, longer setiforms toward apex; lateral lobes ventrally with sparse chaetiforms near proleg base; anal division with 4–6 prominent setiforms along apex of median lobe; substernal setae digitiform, pale, 15–20 in number.

Pupa (Figs. 17, 143–145): Measurements, male (N = 20): Total length 3.7 mm (3.5–3.9), width 2.0 mm (1.6–2.2); female (N = 15): Total length 4.1 mm (4.0–4.3), width 2.3 mm (2.2–2.4).

Body outline roughly ellipsoid, broadly truncated anteriorly. Abdominal tergites sometimes with double row of small, submedian tubercles (remnants of larval tubercles). Integument: Abdominal tergites set with poorly developed papillae consisting mostly of circular patches of spinules (similar to *B. cherokea*); under light microscopy, each patch may have appearance of

light-colored papilla or papilla surrounded by light-colored halo; patches uniformly distributed on abdominal segments; spinule patches sparse on metatergite. Cuticle homogeneous, without reticulate pattern but with minute furrows or punctures between spinule patches. Branchial sclerite without papillae. Anal tergite wrinkled. Middle lamellae of respiratory organ narrow basally, width at midpoint approximately half width of outer lamellae.

Adult male: Size: Small to medium-sized. Measurements (N = 5): Total length 3.4 mm (3.1–3.6), wing length 4.3 mm (4.0–4.5), width 1.4 mm (1.2–1.5).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	2.7 (2.6–2.9)	2.8 (2.6–2.9)	3.7 (3.4–4.0)
tibia	2.5 (2.3–2.6)	2.4 (2.2–2.6)	3.5 (3.2–3.5)
tarsus 1	1.3 (1.2–1.4)	1.2 (1.1–1.3)	1.2 (1.0–1.3)
2	0.6 (0.6–0.7)	0.6 (0.5–0.6)	0.4
3	0.4	0.4 (0.3–0.4)	0.3
4	0.2	0.2	0.2
5	0.2	0.2	0.2

Head (Fig. 49): Structure: Normal type, dichoptic. Clypeus length/width = 2.7. Eyes approximate dorsally, interocular distance approximately 0.1 mm; eye divided, dorsal division much smaller than and mostly contiguous with ventral division (callis oculi absent); dorsal division with 12 or 13 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.42× head width; mandibles absent; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.4–1.4–3.7. Antenna with 15 articles, flagellomeres somewhat barrelshaped proximally, cylindrical distally; ultimate flagellomere 1.2× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomere 1 glabrous basally but densely setose apically, f2–f12 setose, f13 setose basally and mostly glabrous apically but terminated in 2 prominent setiforms; scape and base of f1 pale, pedicel and remaining flagellomeres concolorous, gray-brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (≈5), parietals (0), occipitals (≈20), verticals (3 or 4), postgenals (8–10).

Thorax and appendages: Tibial spurs 0–0–1; hindleg spur ≈0.12 mm; base of hind tarsomere 1 with two or three dark, spiniform sensilla. Leg-segment proportions: foreleg—34:32:16:8:5:3:3, midleg—36:31:15:8:5:3:3, hindleg—39:37:13:4:3:2:2. Chaetotaxy: Scutum mostly glabrous; scutellum with cluster of 10–15 chaetiforms laterally, mostly glabrous medially.

Coloration: Frons and face mostly light brown, clypeus pale. Thorax mostly light brown, pruinose. Mesoscutum and scutellum light brown; pleuron brown to light brown anteriorly (episternum, anterior margin of anepimeron), mostly pale posteriorly. Forecoxa light brown; other coxae pale. Abdominal tergites light brown, sternites pale, pleural membrane broad, pale.

Terminalia (Figs. 51–52): Abdominal segment VIII reduced, mostly membranous; tergite consisting of basal ligulate sclerite extended to pleural region; pleurites and sternite undifferentiated. Epandrium simple, broadly convex posteromedially, with setiform sensilla mostly along posterior margin. Cerci well developed, parallel; set with setiform sensilla; interlobular depression narrowly U shaped; individual cercal lobes narrow, longer than broad, inner margin straight, posterior margin without conspicuous lobes or processes but acutely pointed apically. Genital capsule broad, slightly longer than wide, posterolateral corners strongly produced. Gonostylus set with numerous setiform sensilla. Aedeagal rods of phallus comprising equal, long, slender filaments with simple apices. Ejaculatory apodeme extended approximately ½ distance to anterior margin of lateral parameral lobes. Parameres: Dorsal paramere opaque, apex incised either side of medial dorsal carina; ventral parameres longer than aedeagal rods, broad throughout, tapered to complex apex with expanded inner wall; lateral par-

ameral lobes large, broad, outer margins slightly emarginate.

Adult female: Size: Small to medium-sized. Measurements (N = 3): Total length 4.7 mm (4.5–4.8), wing length 5.5 mm (5.2–5.5), width 1.7 mm (1.6–1.8).

Leg-segment lengths:	foreleg	midleg	hindleg
femur	3.3 (3.2–3.4)	3.0 (3.0–3.1)	4.3 (4.1–4.5)
tibia	2.8 (2.7–2.9)	2.7 (2.6–2.8)	4.0 (3.8–4.1)
tarsus 1	1.2 (1.2–1.3)	1.2 (1.2–1.3)	1.6 (1.5–1.7)
2	0.7	0.6 (0.6–0.7)	0.6 (0.5–0.6)
3	0.4	0.4	0.4
4	0.2 (0.2–0.3)	0.2 (0.2–0.3)	0.2
5	0.3	0.3	0.3

Head (Fig. 48): Structure: Normal type, subholoptic. Clypeus length/width = 2.4. Eyes approximate dorsally, interocular distance approximately 0.03 mm; eye divided, dorsal division subequal in size to and well separated from ventral division (callis oculi broad); dorsal division with 15 or 16 rows of ommatidia along mid-meridian; dorsal ommatidia larger than ventral in diameter. Free portion of proboscis about 0.43× head width; mandibles present; palpi with 5 palpomeres, distal 4 palpomere proportions 1.0–1.2–1.2–3.3. Antenna with 15 articles, flagellomeres cylindrical; ultimate flagellomere 1.6× length of penultimate flagellomere; scape and pedicel with several prominent setiforms, flagellomeres 1–12 sparsely set with setiforms, f13 mostly glabrous, terminated in 2 prominent setiforms; scape, pedicel, and flagellomeres concolorous, brown. Chaetotaxy: Setiform groups as follows (number per side): clypeals (10–15), parietals (<10), occipitals (≈15), verticals (2 or 3), postgenals (≈10).

Thorax and appendages: Tibial spurs 0–0–2; spurs asymmetrical, one each long (0.15 mm) and short (0.07 mm); base of hind tarsomere 1 with ≈5 dark, spiniform sensilla. Leg-segment proportions: foreleg—37:31:13:8:4:2:3, midleg—36:32:14:7:5:2:4, hindleg—38:35:14:5:4:2:3. Chaetotaxy: Scutum mostly glabrous, but with a few scattered chaetiforms in prescutal area and posterolaterally; scutellum with cluster of 10–15 chaetiforms laterally, mostly glabrous medially.

Coloration: Frons and face mostly light brown, clypeus pale. Thorax mostly light brown, pruinose. Mesoscutum and scutellum brown; pleuron brown anteriorly (episternum, anterior margin of anepimeron), light brown to pale posteriorly. Forecoxa brown; other coxae pale. Abdominal tergites, sternites, and pleural membrane brown.

Terminalia (Fig. 50): Posterior margin of sternite VIII broadly bilobate, medial depression poorly developed, broadly V shaped. Sternite IX (genital fork) broadly U shaped, without sclerotized extensions. Hypogynial plate broad basally, narrowed slightly to apical valves; individual valves subpentagonal, truncate apically; inner margins of valves parallel basally, divergent apically, outer margins angulate. Accessory gland narrow, elongate, and extended to level of spermathecae basally, expanded and teardrop-shaped distally. Spermathecae 3 in number; corpora ovoid to kidneyshaped, longer than wide, with short necks; ducts short, uniformly sclerotized and unpigmented. Chaetotaxy: Sternite VIII without setiforms; hypogynial plate pruinose; epiproct with 2 prominent setiforms apically.

Type material.—Holotype [adult male, reared]: UNITED STATES. NORTH CAROLINA: *Swain Co:* Oconaluftee R, GSMNP, 35°32′N 83°17′W, 22 May 1992, coll. G.W. Courtney, emerged 29 May. Specimen pinned, genitalia in glycerin microvial [USNM]. Allotype [adult female, reared]: *Clay Co:* Rock House Ck nr Fires Ck, 35°06′N 83°50′W, 20 May 1995, coll. G.W. Courtney, emerged 25 May; pinned, genitalia in glycerin microvial [USNM]. Paratypes: same data as holotype [10 instar IV L (EtOH), 2 male and 4 female P (EtOH), 1 male and 2 female A, reared (pinned)]; 18 May 1995 [2 instar IV L (EtOH), 6 male and 6 female P (EtOH), 4 male and 3 fe-

male A, reared (pinned)]; *Clay Co:* Fires Ck @ FS Rd 340A, 35°06′N 83°50′W, 20 May 1995 [4 instar IV L (EtOH), 8 male and 4 female P (EtOH), 4 male A (pinned)]; Rock House Ck nr Fires Ck, 35°06′N 83°50′W, 20 May 1995 [1 female A (pinned)]; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W, 22 May 1992 [10 instar IV L (EtOH), 10 male and 4 female P (EtOH)]. All paratypes collected by G.W. Courtney, deposited in CUAC, ISU, and USNM.

Other material examined.—UNITED STATES. GEORGIA: *Lumpkin Co:* Dicks Ck nr Waters Ck, 34°41′N 83°56′W, 12 April 1993 [L]; *Towns Co:* Tallulah R nr Tate Branch, 34°57′N 83°33′W, 12 April 1993 [L]; *Union Co:* Helton Ck below falls, 34°45′N 83°53′W, 12 April 1993 [L]; *White Co:* Chatahoochee R nr Martin Branch, 34°44′N 83°45′W, 12 April 1993 [L]; Dukes Ck @ FS Rd 244, 34°42′N 83°47′W, 12 April 1993 [L]; NORTH CAROLINA: *Clay Co:* Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W, 1 May 1991 [L], 10 June 1995 [Pex]; Buck Ck nr confl Park Ck, 35°03′N 83°35′W, 22 April 1991 [L], 1 May 1991 [L]; Fires Ck @ FS Rd 340A, 35°06′N 83°50′W, 20 May 1995 [LPA]; Fires Ck @ Picnic Area, 35°05′N 83°51′W, 25 April 1994 [L]; Leatherwood Falls, 35°05′N 83°51′W, 20 May 1995 [A]; Rock House Ck nr Fires Ck, 35°06′N 83°50′W, 20 May 1995 [LPA]; *Graham Co:* Little Santeetlah Ck @ Joyce Kilmer, 35°21′N 83°55′W, 25 April 1994 [L]; Sand Ck @ FS Rd 81, 35°20′N 83°58′W, 25 April 1994 [L]; Santeetlah Ck @ FS Rd 81, 35°20′N 83°54′W, 25 April 1994 [LP]; Santeetlah Ck nr Wright Ck, 35°20′N 83°56′W, 25 April 1994 [L]; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W, 30 April 1991 [L], 25 April 1992 [L], 22 May 1992 [LP], 24 April 1994 [LP]; Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W, 24 April 1992 [L]; Cataloochee Ck @ lower Xing, GSMNP, 35°40′N 83°04′W, 30 April 1991[L], 24–25 April 1992 [L], 22 May 1992 [L], 7 April 1995 [L], 30 April 1995 [L], 18 May 1995 [LP], 6 May 1997 [L], 15 May 1998 [LPA], 12 April 1999 [L]; Cold Springs Ck, Pisgah NF, 35°44′N 83°01′W, 24 April 1994 [L]; Little Cataloochee Ck, GSMNP, 35°40′N 83°04′W, 25 April 1992 [L]; Lost Bottom Ck, GSMNP, 35°38′N 83°08′W, 6 May 1997 [LP], 12 April 1999 [L]; Palmer Ck, GSMNP, 35°38′N 83°08′W, 24 April 1992 [L]; "Pretty Hollow" Ck, GSMNP, 35°38′N 83°07′W, 12 April 1999 [L]; W Fk Pigeon R @ Sunburst, 35°22′N 82°56′W, 25 May 1995 [P]; *Swain Co:* Deep Ck, GSMNP, 35°27′N 83°26′W, 24 April 1992 [L]; Oconaluftee R, GSMNP, 35°32′N 83°17′W, 24 April 1992 [L], 22 May 1992 [LPA], 24 March 1995 [L], 7 April 1995 [L], 30 April 1995 [LP], 18 May 1995 [LPA], 15 April 1996 [L], 8 May 1996 [LP]; Raven Fork, GSMNP, 35°31′N 83°17′W, 24 April 1992 [L]; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W, 24 April 1994 [L]; TENNESSEE: *Monroe Co:* Tellico R nr Ranger Station, 35°20′N 84°13′W, 25 April 1994 [L]; VIRGINIA: *Washington Co:* Straight Creek, Mt Rogers, 36°38′N 81°43′W, 29 April 1991 [L—identification tentative]

Etymology.—From the Latin for "tubercles" (*tuberosus*), in reference to the two distinctive rows of dorsal tubercles on the larvae.

Distribution (Fig. 174).—*Blepharicera tuberosa* is one of several species endemic to the southern Blue Ridge. A possible record from the Mount Rogers area suggests that the species is more widespread. I predict that its distribution extends farther west in Georgia and Tennessee. The distribution of *B. tuberosa* overlaps broadly with that of *B. coweetae* and *B. williamsae*.

Bionomics.—*Blepharicera tuberosa* occurs primarily in medium-sized (third- and fourth-order) streams, including some with fairly extensive riparian cover. Larval and pupal habitats typically are characterized by moderately high current velocity (>1 m/s). *Blepharicera tuberosa* is primarily a spring species. At most sites, eggs apparently begin hatching in late March or April. Early

instar larvae often overlap temporally with mature larvae of *B. cherokea* and the winter species *B. coweetae* and *B. williamsae*. Phenological data suggest that most populations are univoltine with relatively synchronous development. At several sites, adults have been collected on riparian vegetation, where they rest on the undersides of leaves.

Remarks.—Although larval *B. tuberosa* superficially resemble those of *B. diminutiva*, the former are easily recognized by the double row of dorsal tubercles. Pupae without remnants of dorsal tubercles are very similar to pupae of *B. cherokea* and *B. corniculata*. All three species lack distinct abdominal papillae (although spinule patches can give appearance of light-colored papillae) and must be distinguished by a combination of characters. Pupae of *B. tuberosa* differ from those of *B. corniculata* in features of the respiratory organs (middle lamellae narrow in *B. cherokea* and *B. tuberosa*) and from pupae of *B. cherokea* in the background microsculpture (*B. corniculata* and *B. tuberosa* pupae with micropunctures between spinule patches). Likewise, adult males show similarities with several other species, notably *B. separata* and *B. diminutiva*, which can be distinguished by minor differences in the shape of the cerci and dorsal parameres.

Blepharicera williamsae Alexander 1953
(Figs. 58, 64, 78, 81, 169–171, 173)

Blepharocera williamsae Alexander 1953: 43 [original designation], 1958: 820 [species list], 1963: 51 [redescription, keys].

Blepharicera williamsae Alexander: Stone 1965:99 [catalog]; Hogue 1978: 23 [redescription, keys, figures]; Carlson 1981: 68 [as bioindicators]; Georgian and Wallace 1983: 1237 [larval ecology]; Hogue and Georgian 1986: 19 [taxonomic notes, keys, figures]; Hogue 1987: 128 [redescription, keys, figures]; Johns 1996: 2 [phenology]; Courtney 1998: 743 [rearing technique].

"*Blepharicera* Larva D": Hogue 1978: 29 [description, records, figure]; Carlson 1981: 68 [as bioindicators].

Diagnosis.—A medium-sized to large *Blepharicera*. Larva: Dorsal secondary sensilla mostly fusiforms, distributed generally over dorsum; color variable but typically with contrasting cranial pattern, light bands typically extended parallel to frontoclypeal apotome; body with dark medial band, its lateral margins not extended onto dorsum of prolegs; lateral muscle scars at margins of these bands. Pupa: Ovoid in shape; abdominal tergites with fine reticulate (areolate) pattern, surface luster very dull (tergites and branchial sclerite); papillae dark, uniformly spaced; lamellae of respiratory organ of subequal width. Adult male: Dorsal and ventral eye divisions subequal in size; cercus with inner margin greatly expanded near base, reaching to or beyond midline; apical margin with prominent, rounded lobe near outer margin. Adult female: 3 spermathecae, ducts uniformly sclerotized and unpigmented; dorsal and ventral eye divisions contiguous (callis oculi absent); distal palpomere elongate (>3× length of penultimate palpomere); number of parietal sensilla >30.

Description.—See Hogue (1987).

Type material.—Holotype [female]: UNITED STATES. TENNESSEE: *Sevier Co:* GSMNP, above Greenbrier Cove, Mount Lecont, 4,200 feet, 5 June 1930, coll. C.P. Alexander [USNM].

Collection localities.—UNITED STATES. GEORGIA: *Lumpkin Co:* De Soto Falls State Park, upper falls, 34°42′N 83°55′W; *Rabun Co:* Reed Mill Ck @ Rd 86, 34°56′N 83°11′W; *Towns Co:* Coleman R nr Tallulah R, 34°55′N 83°52′W; Tallulah R nr Tate Branch, 34°57′N 83°33′W; *Union Co:* Nottley Falls, 34°44′N 83°55′W; NORTH CAROLINA: *Avery Co:* trib Elk River, 36°09′N 81°57′W; *Clay Co:* Big Tuni Ck 1mi above Tusquitee R, 35°06′N 83°41′W; Buck Ck @ Rd 350 Xing, 35°05′N 83°36′W; Buck Ck nr confl Park Ck, 35°03′N 83°35′W; Fires Ck @ Picnic Area, 35°05′N 83°51′W; Park

Ck nr confl Buck Ck, 35°03′N 83°35′W; Rock House Ck nr Fires Ck, 35°06′N 83°50′W; trib Buck Ck @ Rd 350, 35°04′N 83°36′W; *Graham Co:* Little Santeetlah Ck @ Joyce Kilmer, 35°21′N 83°55′W; Panther Ck, Nantahala NF, 35°23′N 83°37′W; Sand Ck @ FS Rd 81, 35°20′N 83°58′W; Santeetlah Ck @ FS Rd 81, 35°20′N 83°54′W; Santeetlah Ck nr Wright Ck, 35°20′N 83°56′W; *Haywood Co:* Big Ck nr CG, GSMNP, 35°45′N 83°07′W; Cataloochee Ck nr Palmer Ck, GSMNP, 35°37′N 83°06′W; Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W; Cataloochee Ck, GSMNP, 35°40′N 83°04′W; Cold Springs Ck, Pisgah NF, 35°44′N 83°01′W; Little Cataloochee Ck, GSMNP, 35°40′N 83°04′W; Lost Bottom Ck, GSMNP, 35°38′N 83°08′W; Palmer Ck, GSMNP, 35°38′N 83°08′W; Pretty Hollow trib, GSMNP, 35°38′N 83°07′W; seep above Cataloochee Ck, GSMNP, 35°39′N 83°04′W; small Ck S of FS boundary, 36°35′N 81°49′W; trib Cataloochee Ck nr CG, GSMNP, 35°38′N 83°05′W; W Fk Pigeon R @ "falls", 35°20′N 82°54′W; W Fk Pigeon R @ Sunburst, 35°22′N 82°56′W; *Macon Co:* Bearpen Ck @ Rd 67, 35°02′N 83°30′W; Bridal Veil Falls below Hwy 64, 35°04′N 83°14′W; Clear Ck, Highlands, 35°00′N 83°12′W; Ck #2, Rd 7276, CHL, 35°03′N 83°26′W; Cullasaja R nr Goldmine Rd, 35°05′N 83°15′W; Curtis Ck @ FS Rd 67, 35°04′N 83°31′W; falls/seep @ Blue Valley Overlook, 35°01′N 83°16′W; Hemp Patch Ck @ FS Rd 67, 35°01′N 83°30′W; Highlands, 35°02′N 83°12′W; Jarrett Ck @ Rd 437, 35°09′N 83°37′W; lower Ball Ck, CHL, 35°03′N 83°26′W; lower Shope Fork, CHL, 35°03′N 83°26′W; N Fk Cold Springs Cove, 35°01′N 83°26′W; Nantahala River nr Curtis Ck, 35°04′N 83°31′W; Roaring Fk @ Rd 437, 35°07′N 83°36′W; seep @ jct Rd 7276, CHL, 35°03′N 83°27′W; Shope Fk @ Rd 7276, CHL, 35°03′N 83°27′W; small Ck below Wayah Crest, 35°09′N 83°34′W; trib Jarrett Ck, Wayah Bald, 35°09′N 83°36′W; upper Ball Ck, CHL, 35°02′N 83°27′W; waterfall ≈0.5 mi E Hwy 67, 35°06′N 83°31′W; Watershed 1, CHL, 35°03′N 83°26′W; Watershed 14, CHL, 35°03′N 83°26′W; Watershed 18, CHL, 35°03′N 83°26′W; Watershed 55, CHL, 35°03′N 83°26′W; *McDowell Co:* Curtis Ck near CG, 35°41′N 82°10′W; trib Curtis Ck above Licklog, 35°42′N 82°11′W; *Swain Co:* falls above Collier Ck, GSMNP, 35°38′N 83°21′W; Oconaluftee R, GSMNP, 35°32′N 83°17′W; *Transylvania Co:* Looking Glass Ck nr falls, 35°17′N 82°46′W; N Fk French Broad R, 35°13′N 82°51′W; SOUTH CAROLINA: *Oconee Co:* Brasstown Falls, 34°43′N 83°18′W; Chattooga R @ Hwy 76, 34°49′N 83°18′W; *Pickens Co:* Carrick's Ck @ Table Rock, 35°01′N 82°42′W; Willis Ck @ Sliding Rock, 35°00′N 82°45′W; TENNESSEE: *Cocke Co:* Groundhog Ck, GSMNP, 35°46′N 83°10′W; Cosby Ck, GSMNP, 35°45′N 83°12′W; trib Cosby Ck, GSMNP, 35°45′N 83°12′W; *Johnson Co:* Fagall Branch, 36°34′N 81°51′W; small Ck nr Backbone Rock, 36°35′N 81°49′W; *Sevier Co:* Greenbrier Cove, GSMNP, 35°42′N 83°23′W; upper Greenbrier Cove, GSMNP, 35°42′N 83°20′W; VIRGINIA: *Washington Co:* Feathercamp Bk nr Mt Rogers boundary, 36°38′N 81°44′W; Straight Creek, Mt Rogers, 36°38′N 81°43′W.

Distribution (Fig. 173).—*Blepharicera williamsae* is widespread in the southern Blue Ridge Mountains, ranging from northern Georgia and South Carolina, to the Mount Rogers area of southwestern Virginia. Its distribution overlaps generally with that of *B. coweetae.*

Bionomics.—In terms of stream conditions, *B. williamsae* is highly variable, second perhaps to *B. similans* among Appalachian species. Like *B. similans, B. williamsae* ranges from headwater trickles and waterfalls to large rivers. However, it seems to occur in relatively more headwater streams than does *B. similans* and typically is rare in large rivers, where another winter species, *B. coweetae,* can predominate. *Blepharicera williamsae* is apparently more tolerant of closed-canopy systems than

most other *Blepharicera*, which might explain its presence in many first-order streams at Coweeta Hydrologic Laboratory. Regardless of stream type, *B. williamsae* is usually restricted to areas of very high flow (>1.5 m/s). *Blepharicera williamsae* is a winter species. At most sites, eggs begin hatching in late December or January. At headwater streams or sites at higher elevation, the activity period often shifts to late spring or early summer. Phenological data suggest that most populations are either multivoltine or univoltine but relatively asynchronous. Adults are often collected from emergent rocks or riparian vegetation, where they rest on the undersides of leaves. Johns (1996) speculated that the larger size of *B. williamsae* might make it a stronger flyer and, therefore, better able to colonize small streams. Although a compelling hypothesis, the general absence of other large species (e.g., *B. coweetae, B. gelida, B. magna*) in small streams suggests size might not be an overriding factor in colonization. Anecdotal data suggest *B. williamsae* adults are relatively long-lived, which could also contribute to vagility. Data on adult longevity are lacking for most species.

Remarks.—*Blepharicera williamsae* is among the more distinctive Appalachian species, especially as pupae and adult males. As discussed under *B. coweetae*, the larvae of this species and *B. williamsae* can be difficult to separate.

Unplaced Specimens

Some specimens examined during this study could not be placed into any recognized species. All were from the extreme southern Appalachians (Alabama and western Georgia), in areas I was unable to sample. The Alabama material is especially compelling because it represents a significant range extension for blepharicerids, is the southernmost Appalachian record for the family, and originated from a site that apparently harbors at least three species. These records include the following:

Alabama. *Talapoosa Co:* Hillabee Ck @ Rt 22 [32°59′N 85°51′W], 8 March 1989, coll. J.H. Epler and W. Garrett [FAMU]. This sample contains nine larvae and two pupae, as follows: (1) Four larvae similar to *B. capitata* and *B. separata*. One is piebald, but the rest have dark cranial sclerites and a uniformly light brown body. All four larvae are unusual in their dense covering of digitiform sensilla. All possess 5–10 pale, substernal setae and relatively indistinct lateral lobes on the anal division. (2) Five larvae of a second species. In one of these, the cranial sclerites are dark anteriorly and pale posteriorly (similar to certain populations of *B. coweetae*), and the body is light brown; this specimen appears to be pharate. The remaining four larvae appear to be the same species as the presumed pharate individual, but the cranial sclerites are dark brown and the trunk is uniformly brown. In all five of these specimens, the cephalothorax and trunk are densely and uniformly set with short fusiforms (i.e., not arranged in clusters). The same larvae possess approximately 45 brownish-gray, substernal setae and relatively weakly developed lateral lobes on the anal division. (3) The two pupae probably are conspecific with the latter five larvae and bear some resemblance to *B. coweetae*. In both pupae, the middle respiratory lamellae are broad and the anal division is slightly wrinkled. The integument is unusual among Appalachian species in that the abdominal tergites and metatergite are densely set with dark papillae dorsally; laterally they are less dense, not arranged in clusters, but in some areas forming rows. (4) Another sample, from 15 June 1988, contains one each male and female, the terminalia of which are mounted on slides but are somewhat damaged. In spite of the latter, the cerci appear to resemble those of *B. tenuipes*. If for no other reason than the date, this specimen probably is not conspecific with the above larvae or pupae.

Georgia. Walker Co: Cloudland Canyon State Park [34°50′N 85°28′W], 8 May 1952, coll. G.S. Walley [CNC, LACM].

The original series apparently includes 27 adults: 20 males and seven females; however, I examined only five of these specimens (four males and one female), which presently are in the LACM collection. All examined specimens are mounted on slides, and the terminalia of each is slightly skewed; despite this, most salient taxonomic features are visible. Hogue (1978) placed these specimens in *B. tenuipes,* but subsequently appeared to have shifted them to *B. coweetae* (based on their placement in the LACM collection). In nearly every major taxonomic feature (e.g., dorsal eye division size, cercal shape, dorsal paramere incisions), the males resemble *B. tenuipes* rather than *B. coweetae.* Despite the resemblance, I am hesitant to place these specimens in *B. tenuipes,* which would represent a southern disjunction of nearly 800km. The preponderance of species that resemble *B. tenuipes* in one or more features (e.g., *B. coweetae, B. gelida, B. hispida*) suggests that certain of these features could be homoplastic. A definitive identification awaits the collection of additional material, including larvae and pupae.

General Discussion

The Blephariceridae are characterized by a variety of morphological and ecological features, many that reflect specialization to life in and around torrential streams. Perhaps because of the common need for certain structural adaptations, these flies can exhibit relatively little morphological variation. Structural homogeneity, especially in immature stages, and concomitant difficulty in identifying species have hindered detailed studies of Appalachian *Blepharicera* (e.g., Georgian and Wallace 1983; Lenat 1993). This difficulty is compounded further by the fact that species determinations often require examination of multiple life stages and sometimes ecological data (e.g., collection date).

As established in previous studies (Hogue 1978, 1987), chaetotaxy remains an important character system for identifying *Blepharicera* larvae. Shape and distribution of dorsal secondary sensilla are surprisingly consistent for many *Blepharicera,* even in species from broad geographical areas and thermal regimes (e.g., *B. similans, B. tenuipes*). In most populations and species, cranial and trunk color patterns also are relatively consistent. However, color should be used with caution, because aberrant individuals are common in some populations and color differences can be striking between pharate and fully sclerotized specimens. As indicated in the larval key (cf. couplets 14 and 15), certain species can be difficult to identify even by combinations of characters. The most problematic populations are in the extreme southern Appalachians (e.g., Chattooga River), where levels of sympatry are exceptional. Although hybridization among congeners has not been recorded in these flies, populations in the southern Appalachians represent prime candidates for such possibilities. Although laboratory breeding may be impractical, other types of investigation (e.g., molecular) could shed light on this issue.

Pupal characters, including abdominal microsculpture and the shape of respiratory lamellae, are among the most consistent and diagnostic features for many species. Again, however, determinations frequently require combinations of characters (cf. *B. cherokea* vs. *B. corniculata*) or geographical information (cf. *B. coweetae* vs. *B. hispida*). The present study has shown remarkable diversity of pupal microsculpture in Appalachian *Blepharicera.* The pupae of other blepharicerid genera show comparable microsculptural diversity (Courtney 2000, and unpublished data), as do those of other torrenticolous groups (Courtney 1990b). Although explanations for microsculptural diversity continue to evade biologists, these features presumably influence flow patterns over the pupal cuticle. Observations of pupal habitat for Appalachian *Blepharicera* fail to show any obvious correlation between environment and microsculptural arrangement. Future hydrodynam-

ic studies might provide insights into the relative importance of environmental versus historical factors in the expression of microsculptural features.

Adult males are perhaps the most reliable stage for species determinations, albeit sometimes only by use of subtle terminalic characters or combinations of terminalic and other characters. Terminalic features (e.g., shape of the cerci and dorsal paramere) are distinct in some species (e.g., *B. magna, B. similans, B. williamsae*), but less so in others (e.g., *B. coweetae* vs. *B. hispida, B. cherokea* vs. *B. appalachiae*). In the latter, combinations of terminalic characters, cranial features (e.g., size of dorsal eye division), and sometimes color must be examined to make species determinations. With few exceptions (*B. capitata, B. similans*), female character systems have provided little taxonomic resolution; however, most studies, including the present investigation, have focused on male terminalia. Future studies of *Blepharicera* and other net-winged midges should include more detailed examination of female terminalia, especially of internal structures.

This is the first revision of Appalachian Blephariceridae to include larvae, pupae, and adults of nearly all known species (pupae and adults unknown only in *B. caudata*). This study has introduced several new character systems, evaluated the taxonomic concepts of Hogue (1978, 1987), and described several new species and previously unknown life stages of described species. In spite of these advances, substantial gaps in our knowledge of the Appalachian fauna remain. The southernmost part of the Appalachian Range (i.e., northwest Georgia and northern Alabama) is especially problematic and poorly studied. Winter samples have provided several new species, but these collections are limited primarily to western North Carolina. I predict that winter and early-spring samples from other areas will provide additional records for described species (e.g., *B. gelida, B. hispida*) and might lead to the discovery of new species. Furthermore, additional study of widespread and ecologically diverse taxa (e.g., *B. similans, B. tenuipes*) should provide insights into the presence of sibling species. The present research has established the framework for such investigations, and has provided the character basis for phylogenetic and biogeographic analyses of the *B. tenuipes* group and all Nearctic *Blepharicera*.

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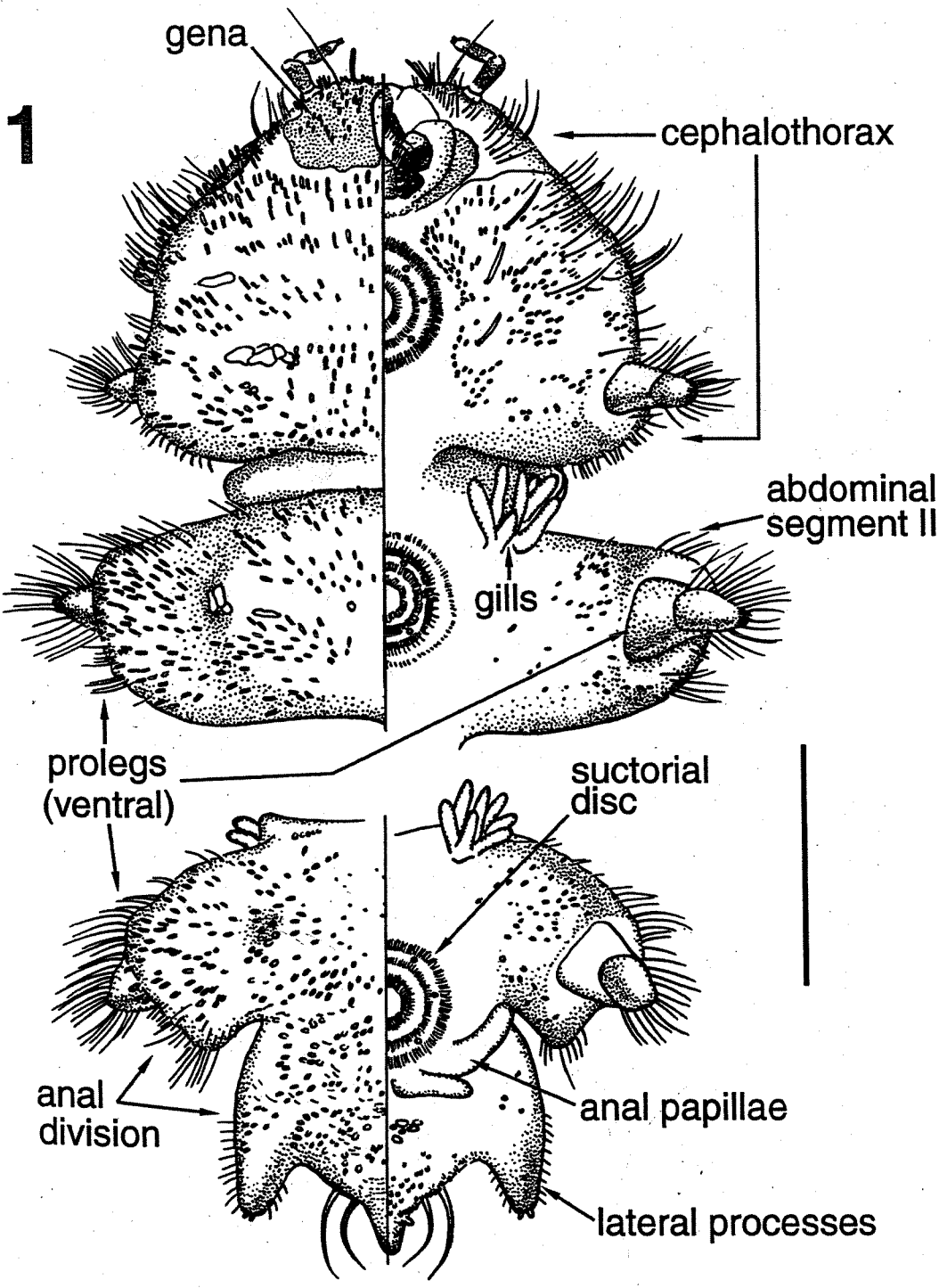
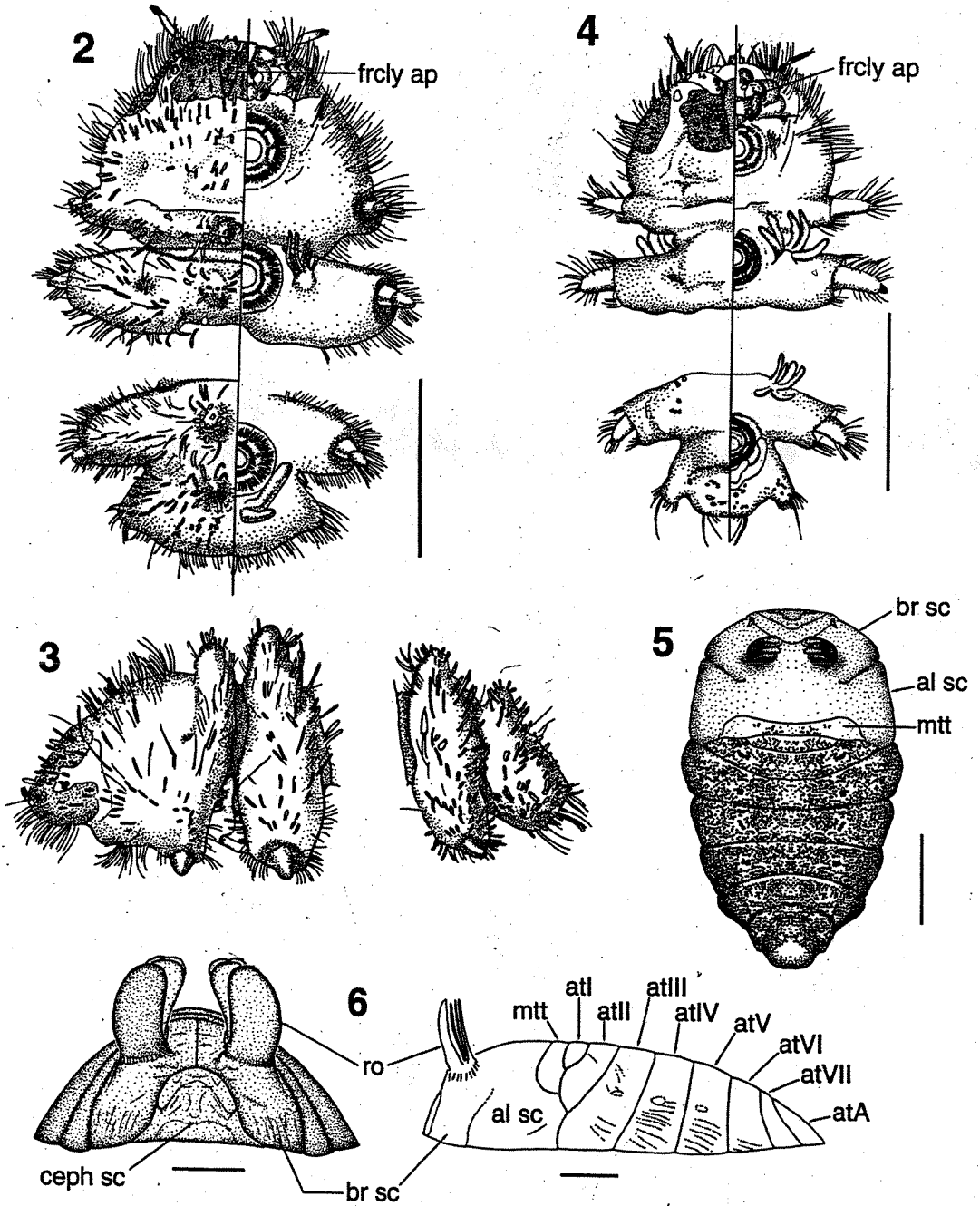
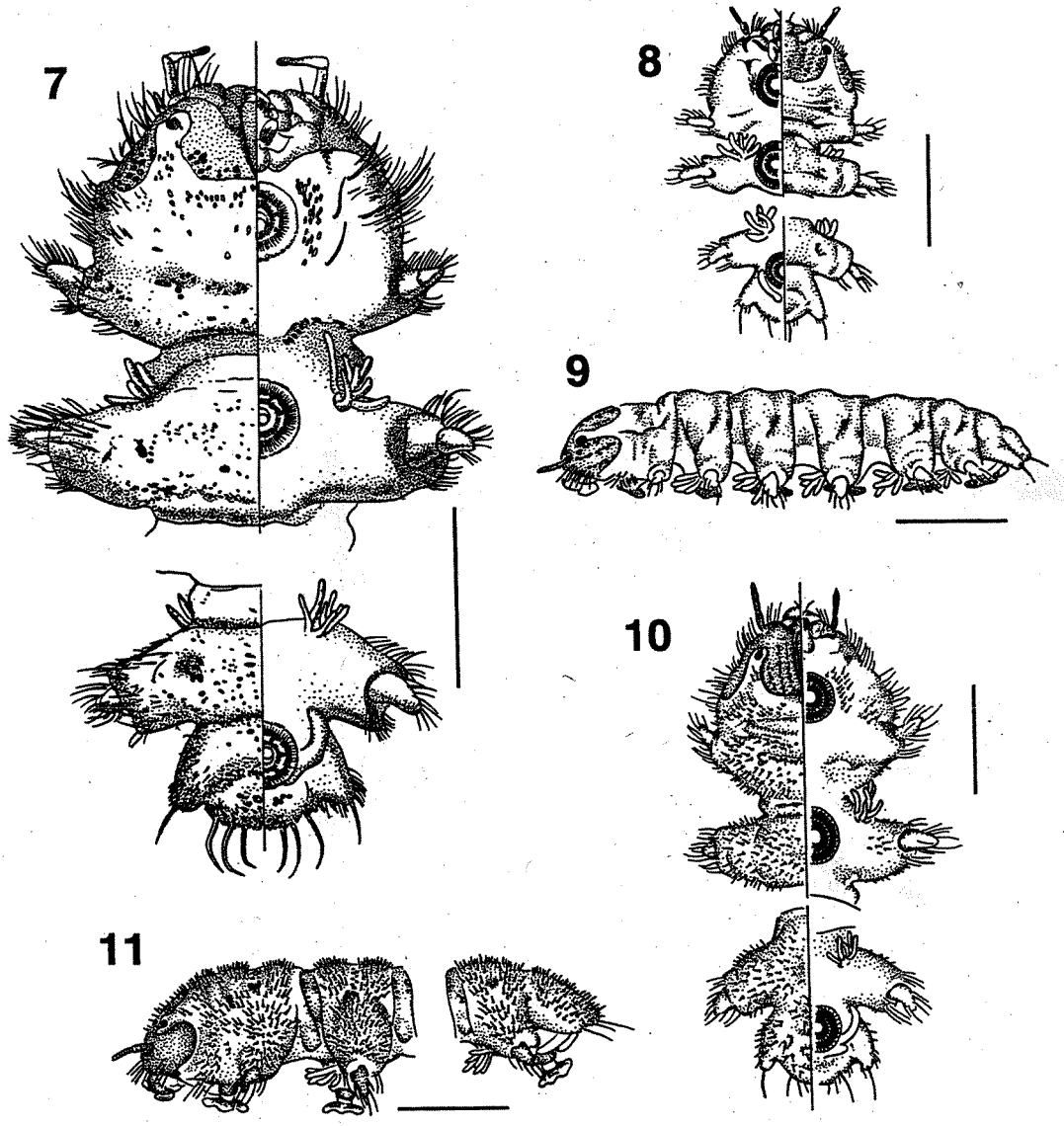


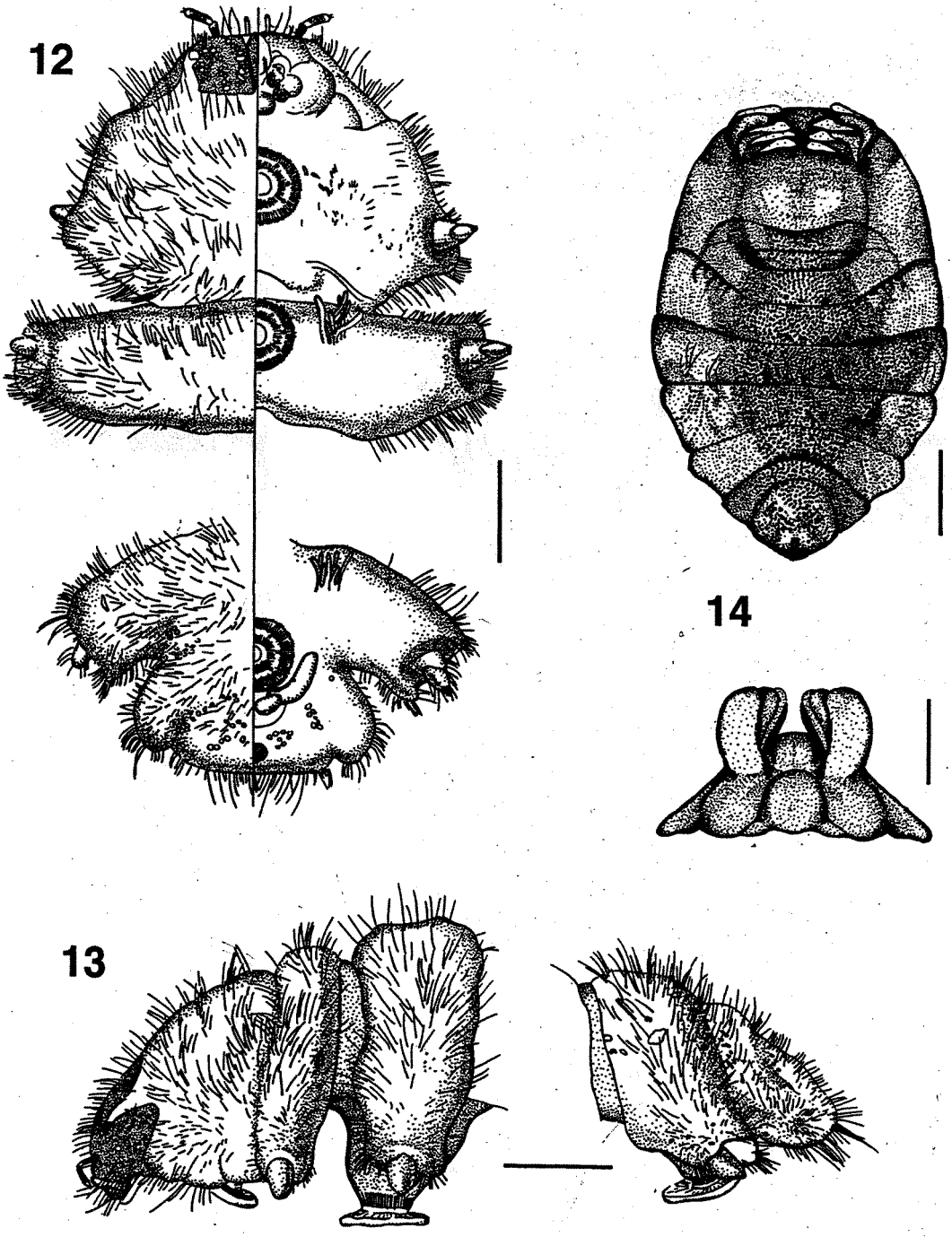
Fig. 1. Cephalothorax, abdominal segment II and anal division of *B. caudata* larva, dorsal (left) and ventral (right) view. Scale bar = 1 mm.



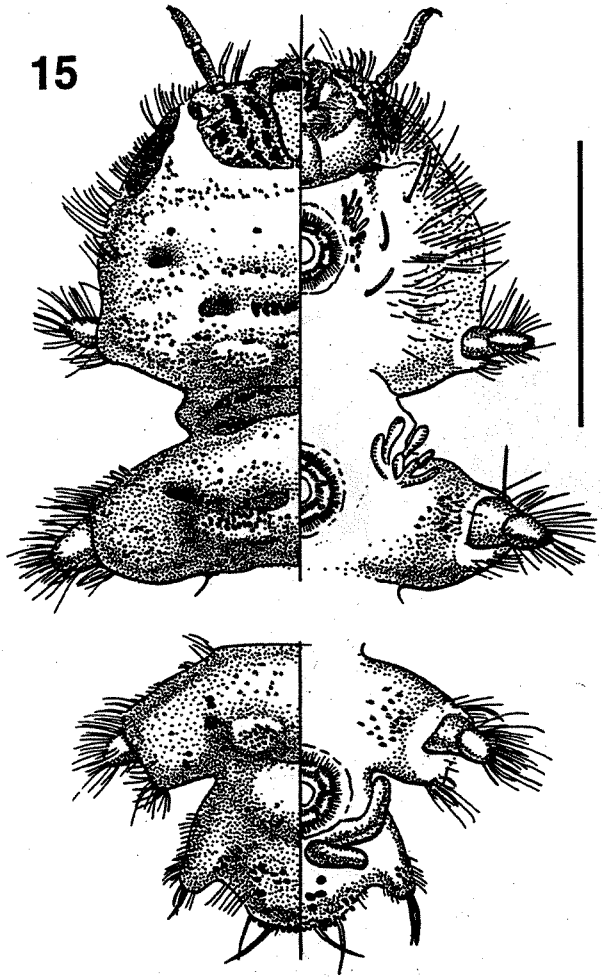
Figs. 2–6. Larvae and pupae of *Blepharicera*. 2, Cephalothorax, abdominal segment II and anal division of *B. capitata* larva, dorsal (left) and ventral (right) view. 3, Cephalothorax, abdominal segment II and anal division of *B. capitata* larva, lateral view. 4, Cephalothorax, abdominal segment II and anal division of *B. chattooga* larva, dorsal (left) and ventral (right) view. 5, *B. chattooga* pupa, dorsal view. 6, *B. magna* pupa, frontal (left) and lateral (right) view. Scale bars = 1 mm. (abbreviations: al sc = alar sclerite; atI-atVII = abdominal tergites I–VII; atA = anal tergite; br sc = branchial sclerite; ceph sc = cephalic sclerite; frcly ap = frontoclypeal apotome).

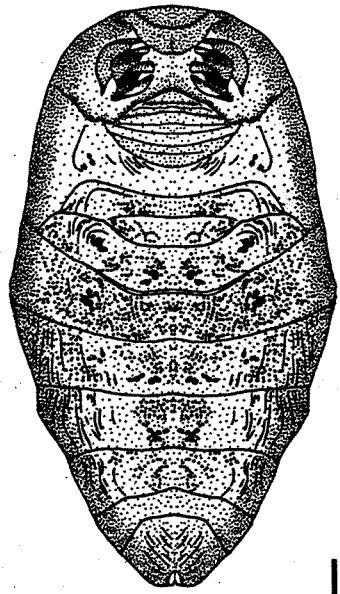


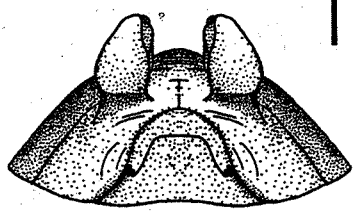
Figs. 7–11. Larvae of *Blepharicera*. 7, Cephalothorax, abdominal segment II and anal division of *B. cherokea* larva, dorsal (left) and ventral (right) view. 8, Cephalothorax, abdominal segment II and anal division of *B. diminutiva* larva, ventral (left) and dorsal (right) view. 9, *B. diminutiva* larva, lateral view. 10, Cephalothorax, abdominal segment II and anal division of *B. hispida* larva, dorsal (left) and ventral (right) view. 11, Cephalothorax, abdominal segment II and anal division of *B. hispida* larva, lateral view. Scale bars = 1 mm.

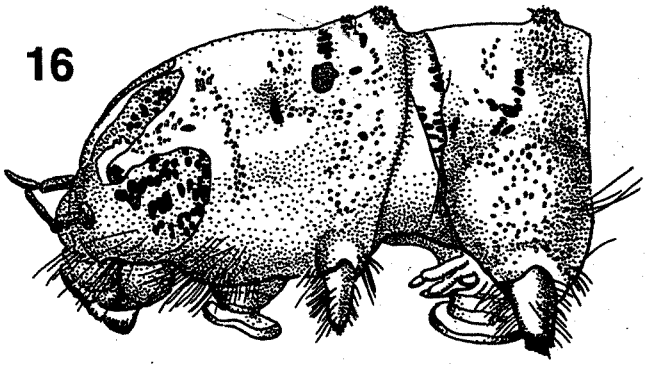


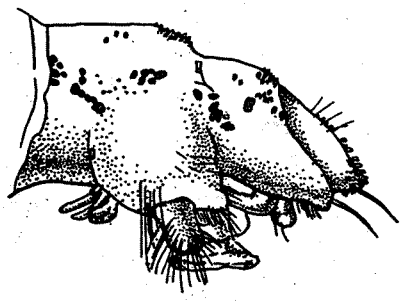
Figs. 12–14. Larvae and pupae of *B. gelida*. 12, Cephalothorax, abdominal segment II and anal division of larva, dorsal (left) and ventral (right) view. 13, Cephalothorax, abdominal segment II and anal division of larva, lateral view. 14, Pupa, frontal (below) and dorsal (above) view. Scale bars = 1 mm.



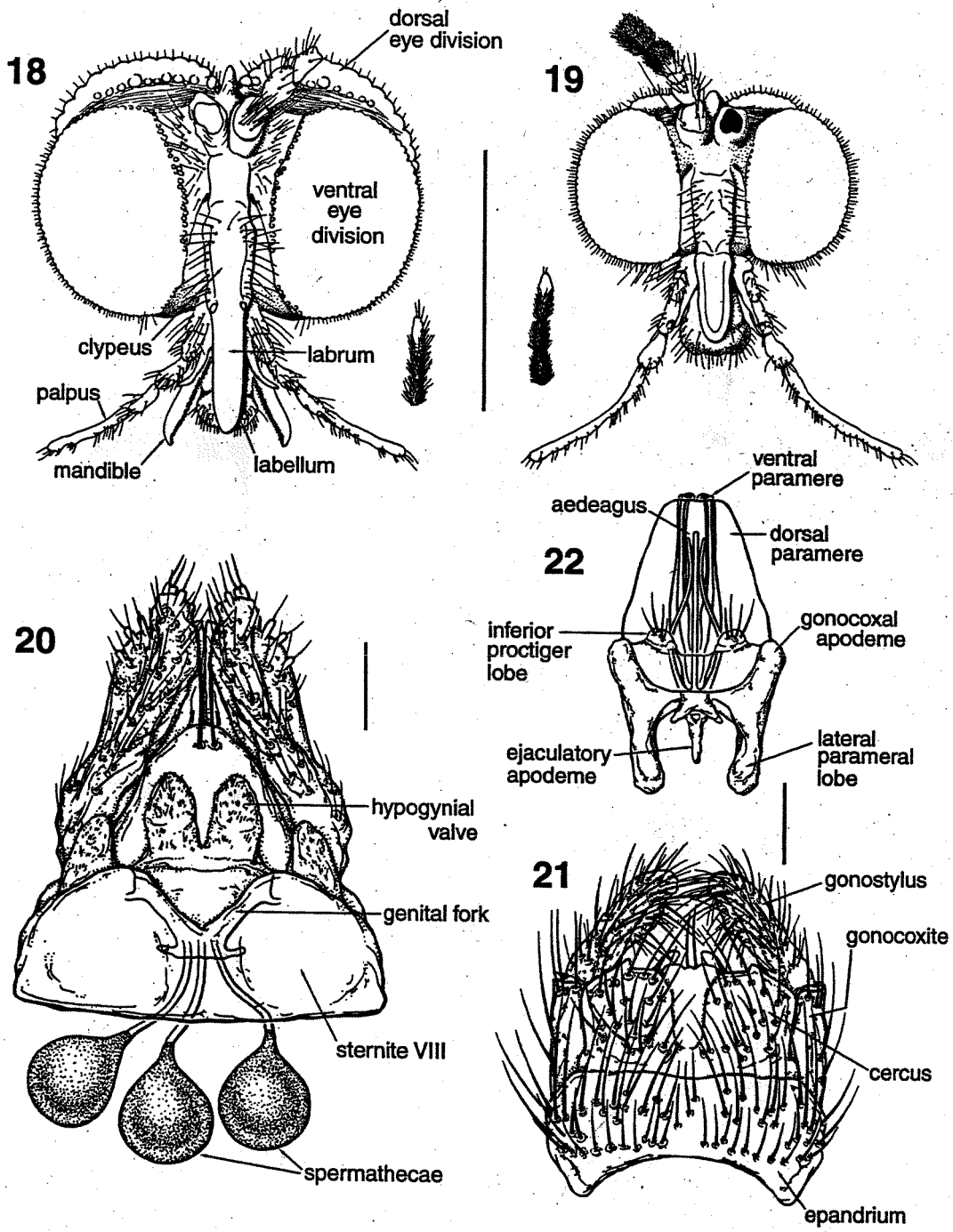




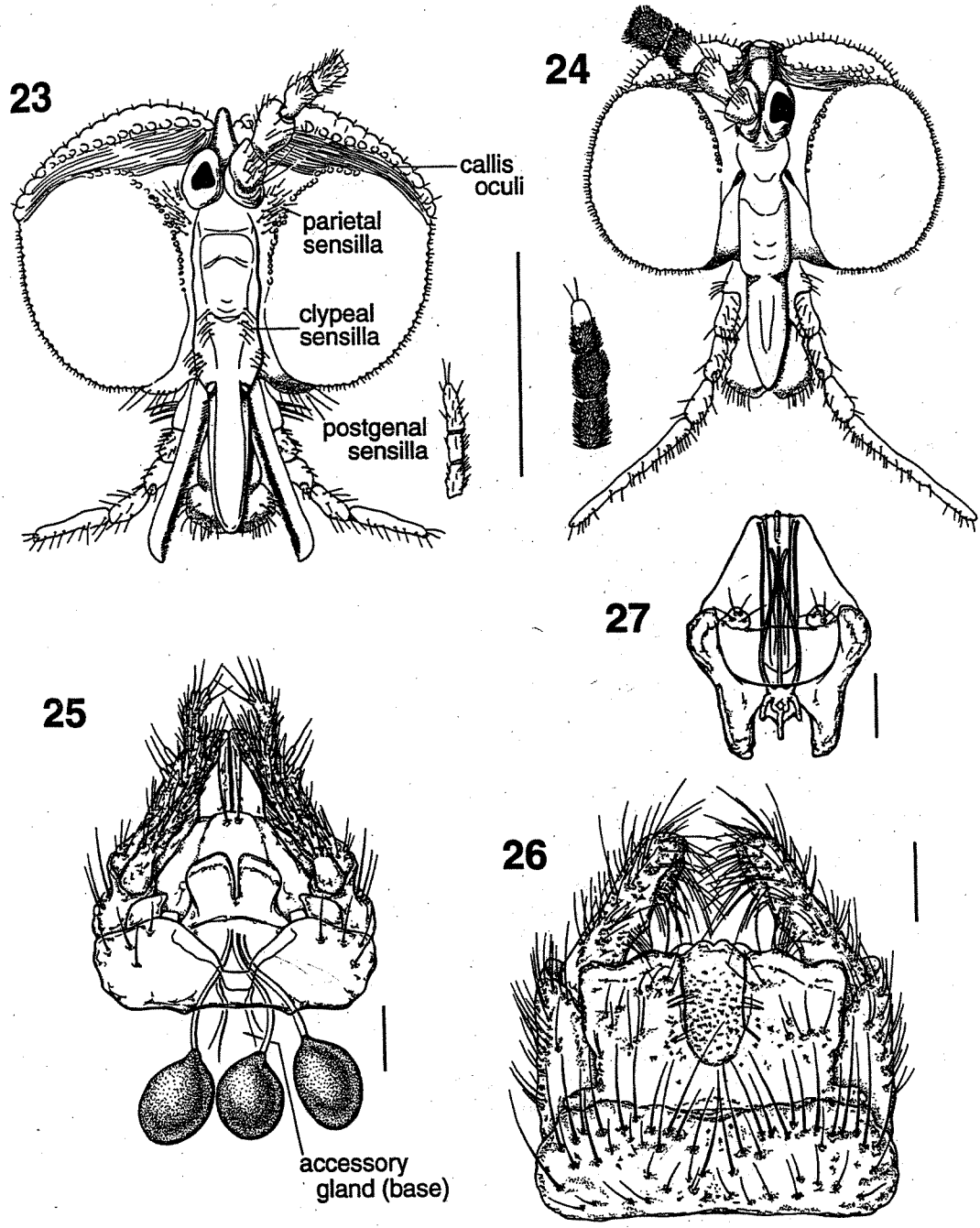




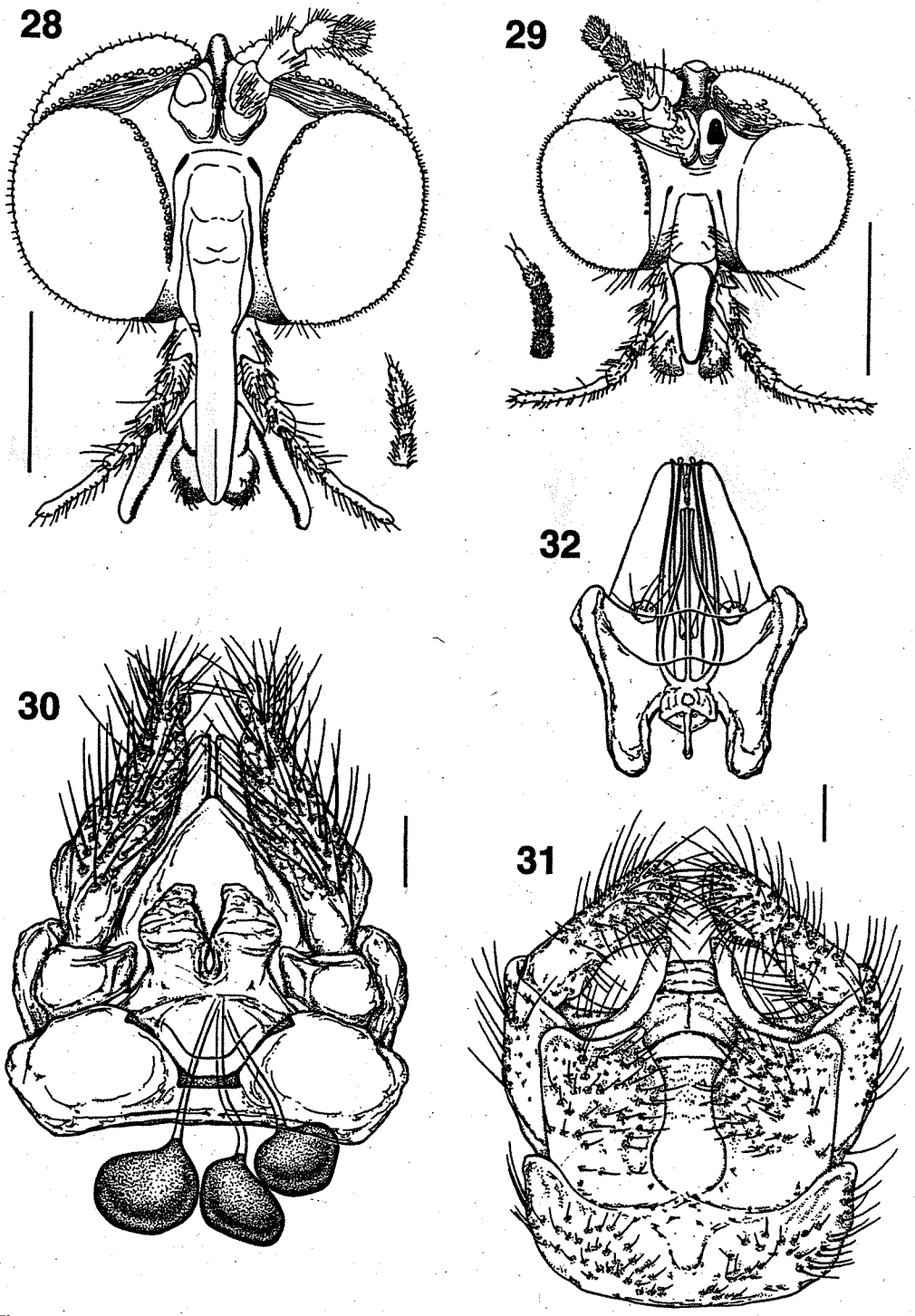
Figs. 15–17. Larvae and pupae of *B. tuberosa*. 15, Cephalothorax, abdominal segment II and anal division of larva, dorsal (left) and ventral (right) view. 16, Cephalothorax, abdominal segment II and anal division of larva, lateral view. 17, Pupa, frontal (below) and dorsal (above) view. Scale bars = 1 mm.



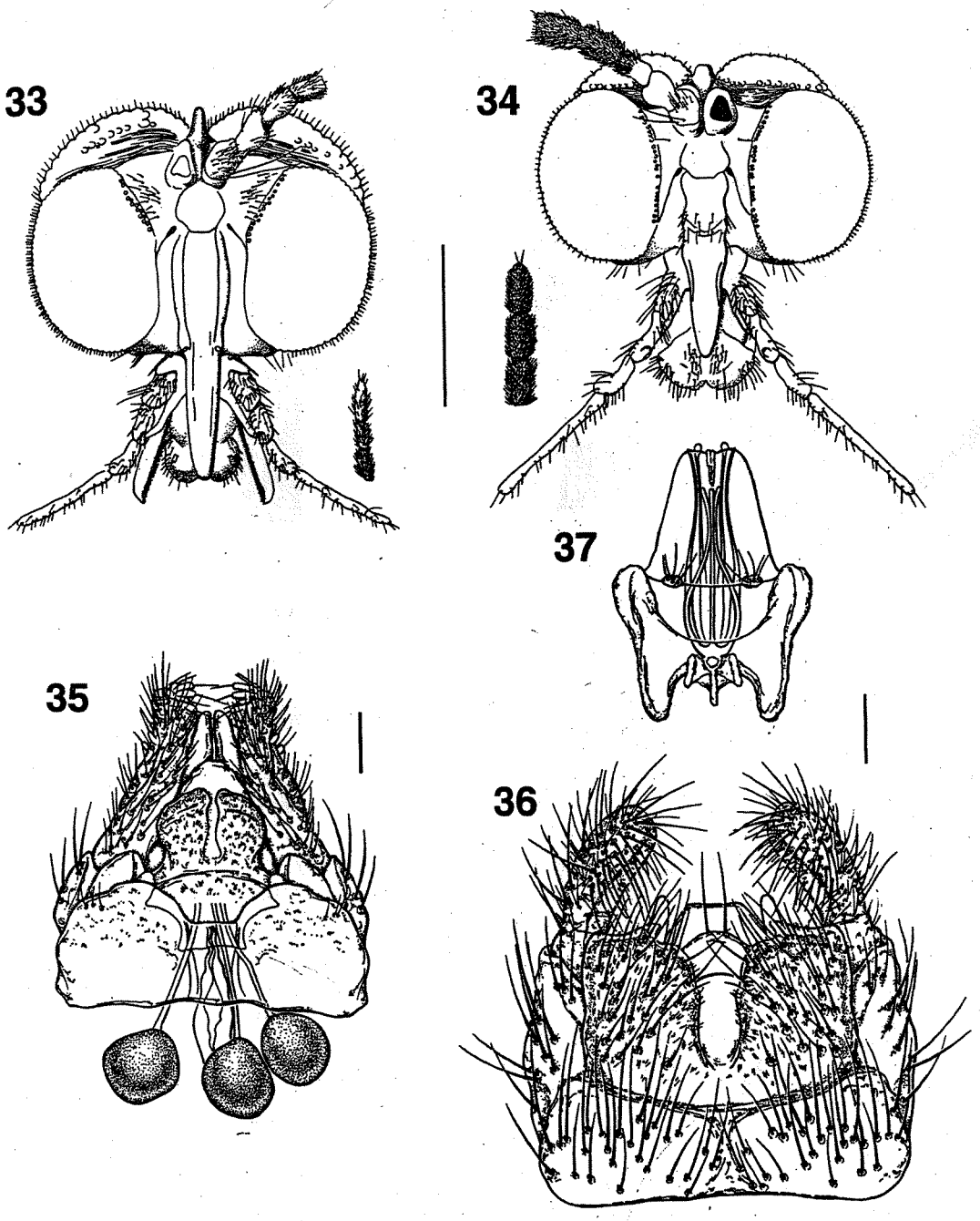
Figs. 18–22. Adults of *B. chattooga*. 18, Female head and antennal apex, frontal view. 19, Male head and antennal apex, frontal view. 20, Female terminalia, ventral view. 21, Male terminalia, dorsal view. 22, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 18–19), 0.1 mm (Figs. 20–22).



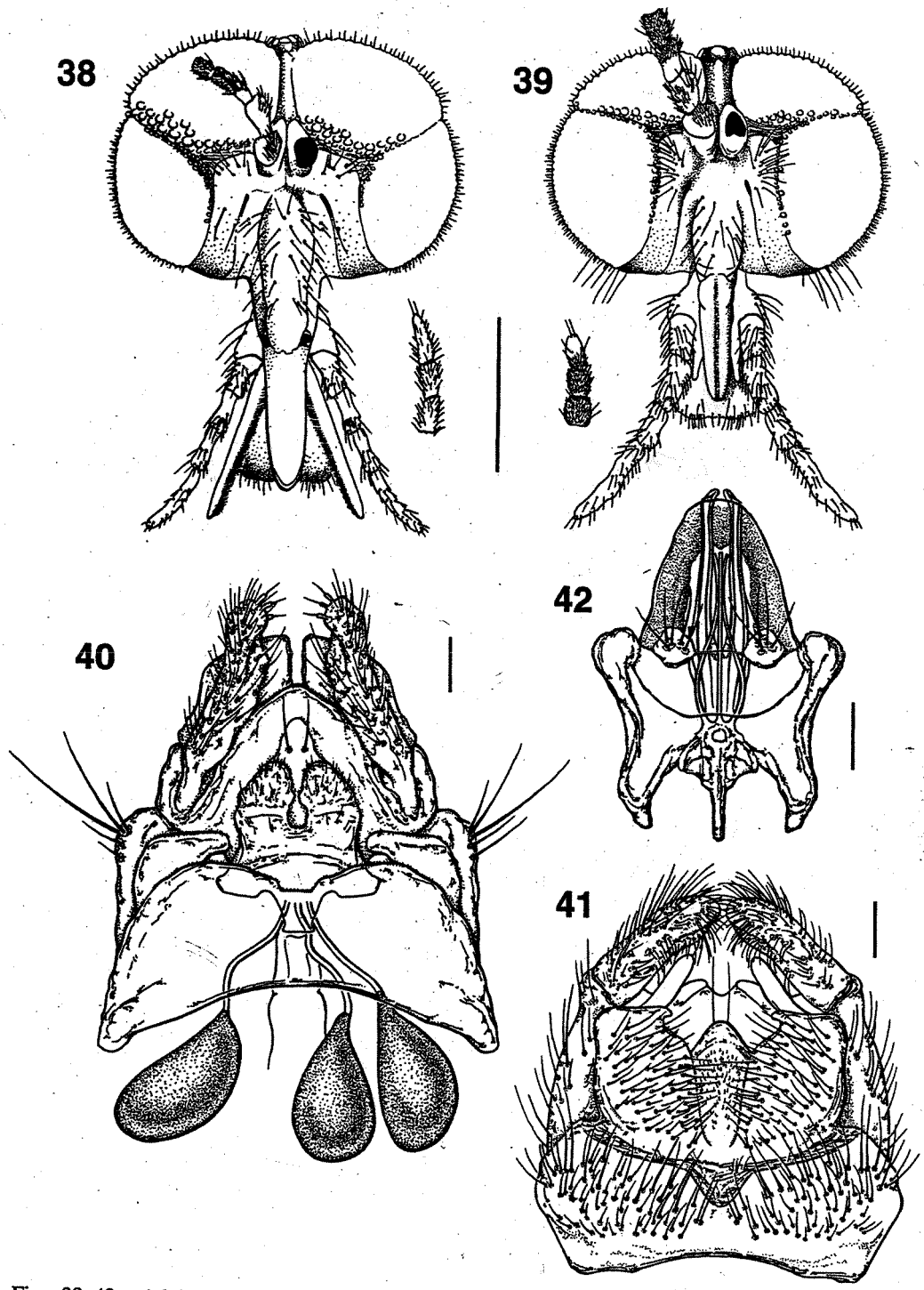
Figs. 23–27. Adults of *B. corniculata*. 23, Female head and antennal apex, frontal view. 24, Male head and antennal apex, frontal view. 25, Female terminalia, ventral view. 26, Male terminalia, dorsal view. 27, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 23–24), 0.1 mm (Figs. 25–27).



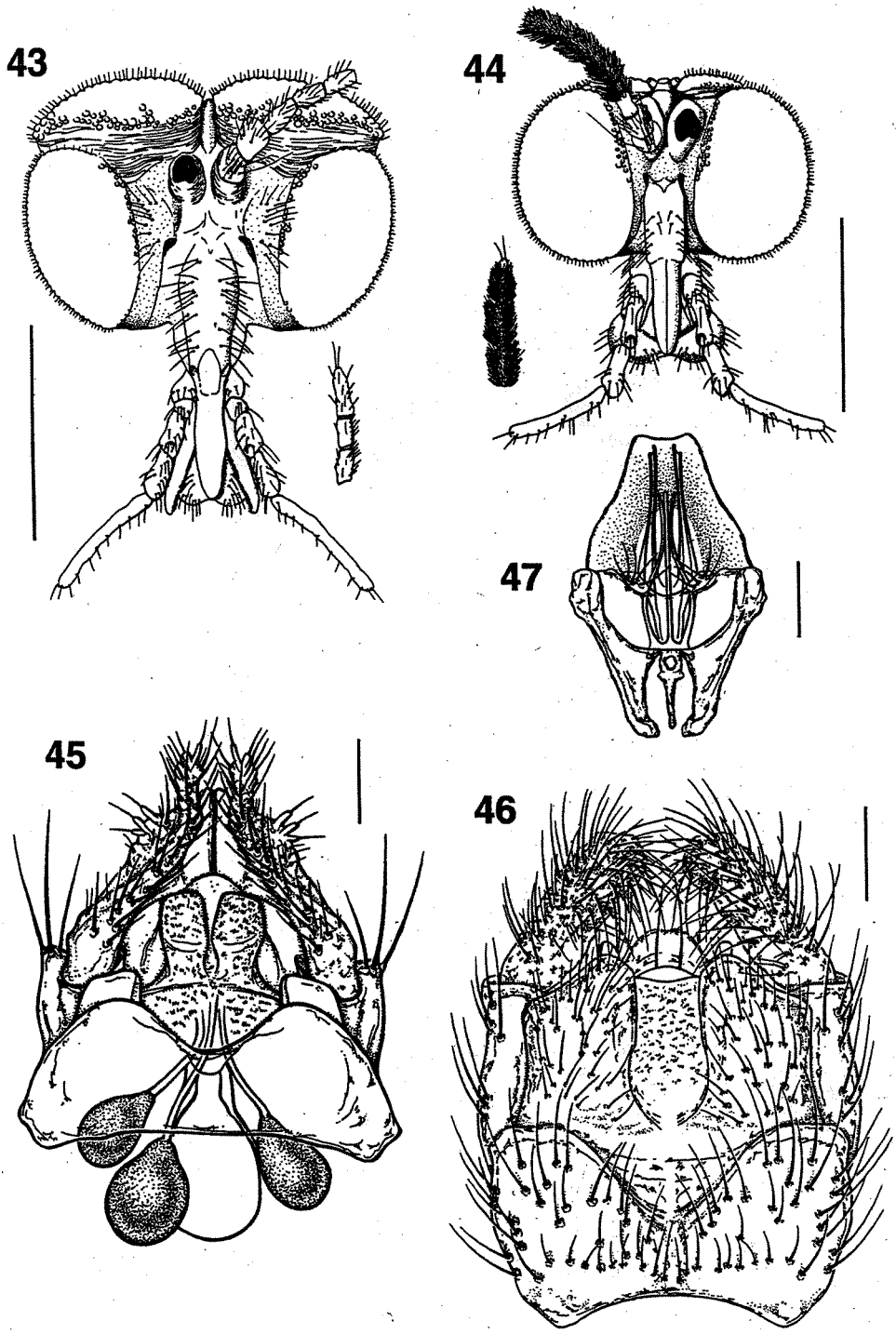
Figs. 28–32. Adults of *B. gelida*. 28, Female head and antennal apex, frontal view. 29, Male head and antennal apex, frontal view. 30, Female terminalia, ventral view. 31, Male terminalia, dorsal view. 32, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 28–29), 0.1 mm (Figs. 30–32).



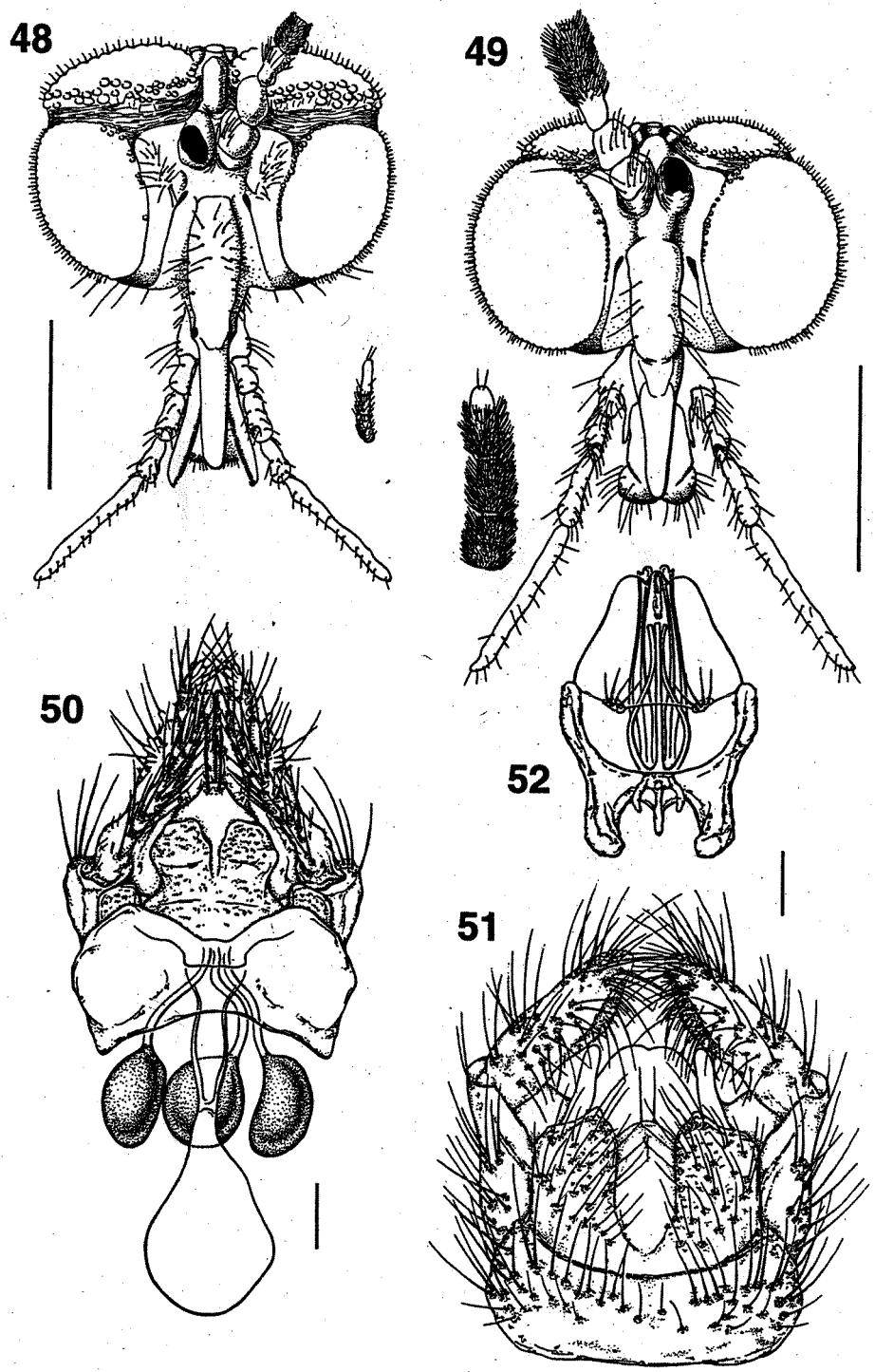
Figs. 33–37. Adults of *B. hispida*. 33, Female head and antennal apex, frontal view. 34, Male head and antennal apex, frontal view. 35, Female terminalia, ventral view. 36, Male terminalia, dorsal view. 37, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 33–34), 0.1 mm (Figs. 35–37).



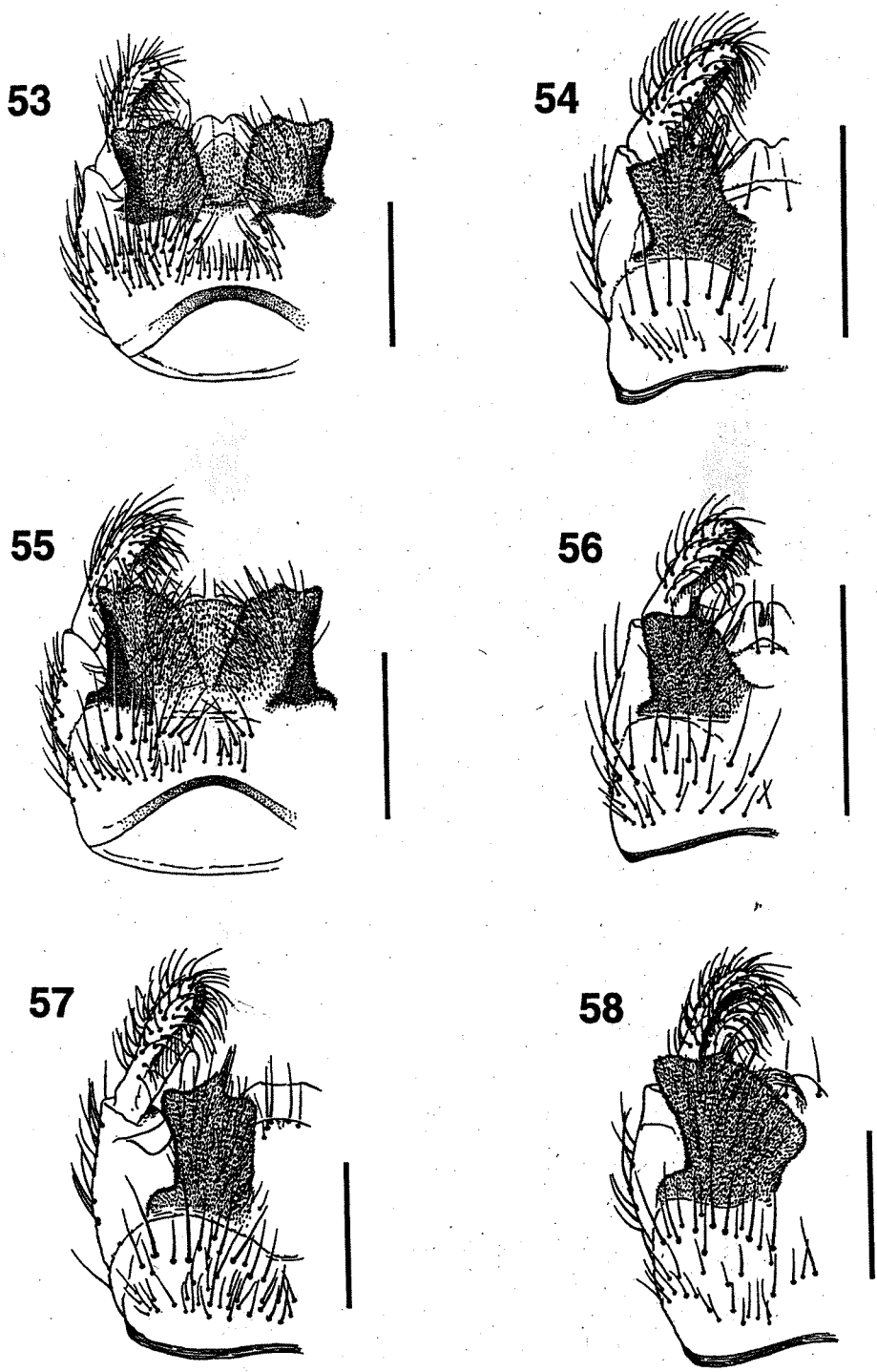
Figs. 38–42. Adults of *B. magna*. 38, Female head and antennal apex, frontal view. 39, Male head and antennal apex, frontal view. 40, Female terminalia, ventral view. 41, Male terminalia, dorsal view. 42, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 38–39), 0.1 mm (Figs. 40–42).



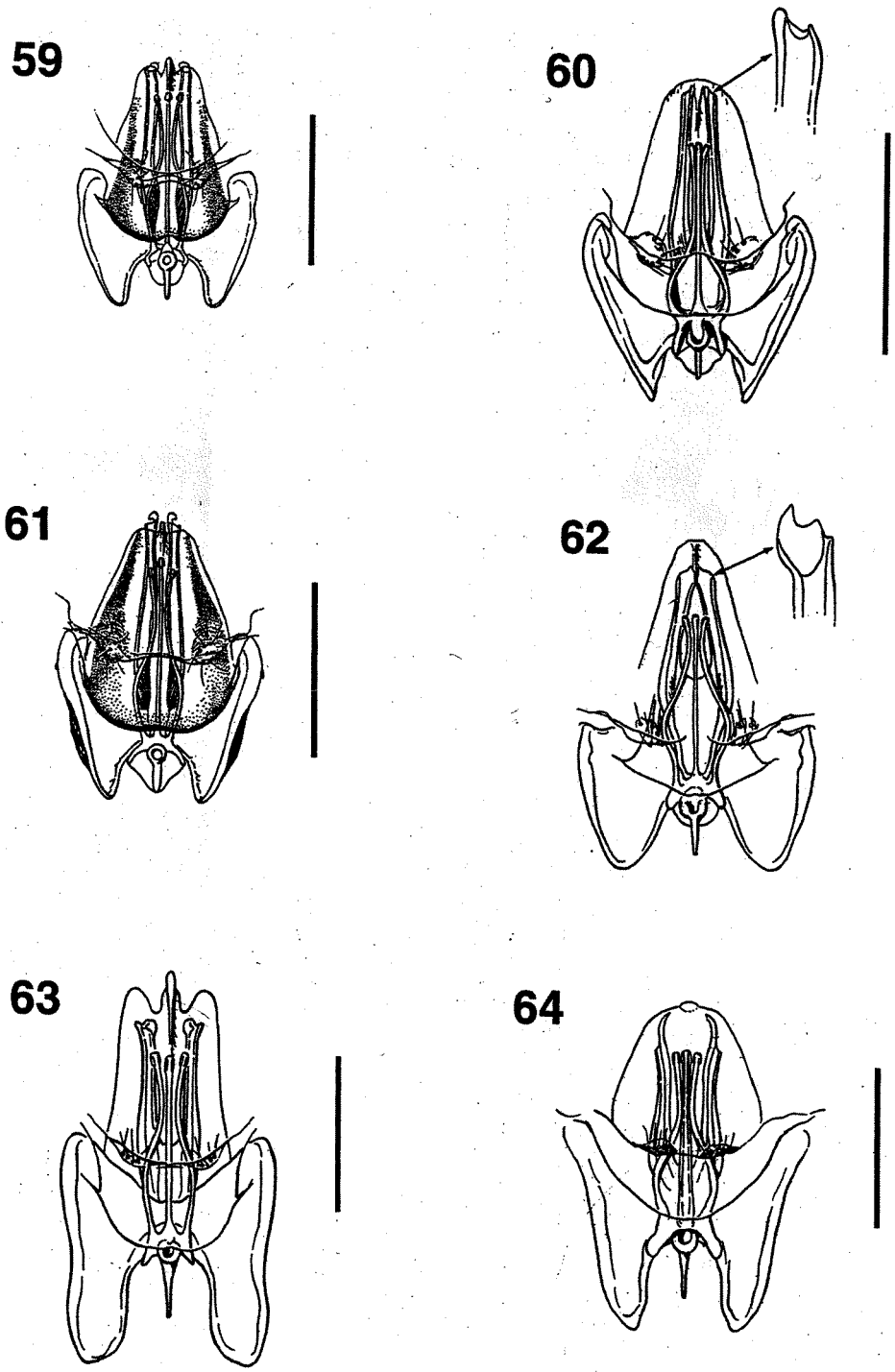
Figs. 43–47. Adults of *B. separata*. 43, Female head and antennal apex, frontal view. 44, Male head and antennal apex, frontal view. 45, Female terminalia, ventral view. 46, Male terminalia, dorsal view. 47, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 43–44), 0.1 mm (Figs. 45–47).



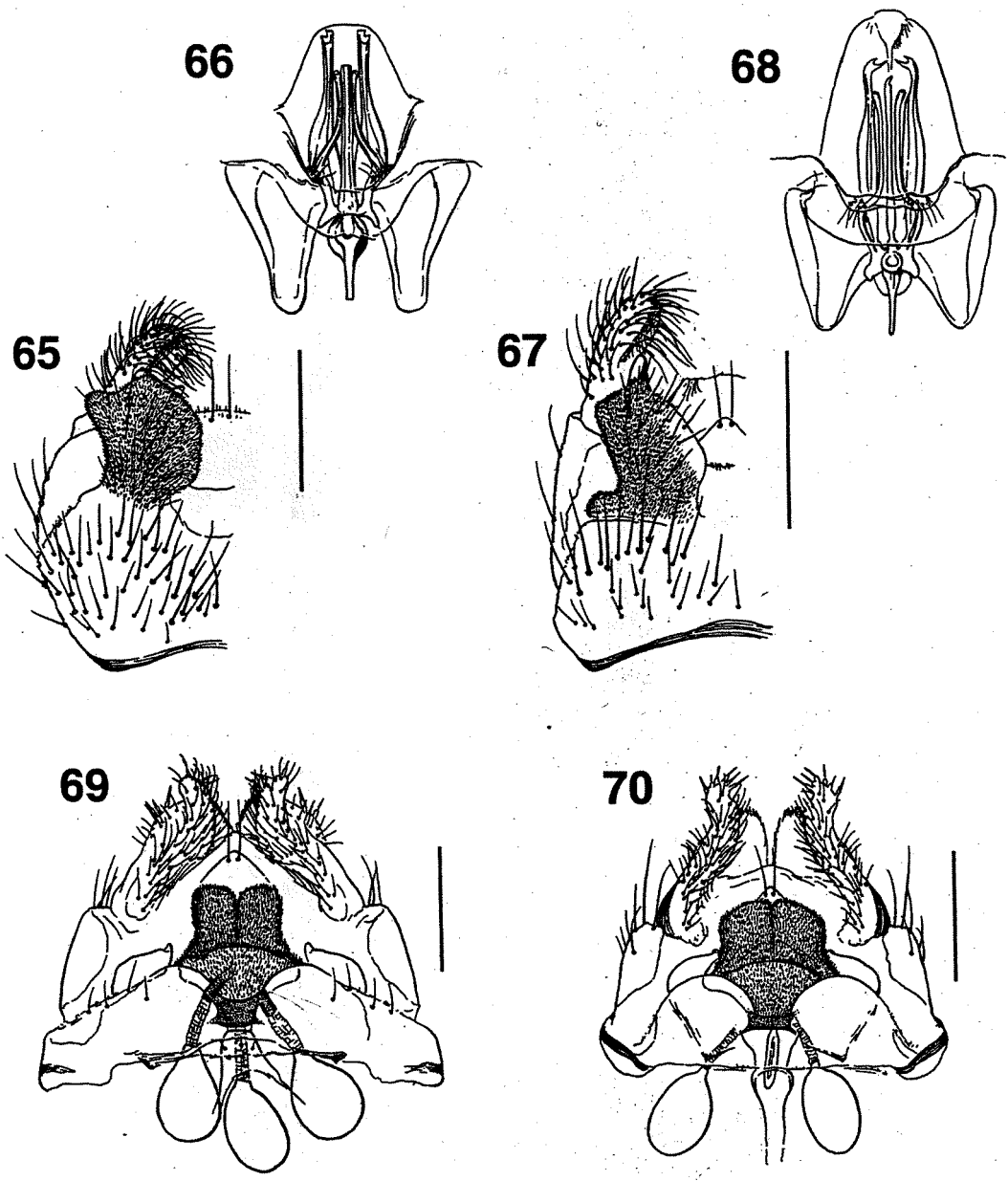
Figs. 48–52. Adults of *B. tuberosa*. 48, Female head and antennal apex, frontal view. 49, Male head and antennal apex, frontal view. 50, Female terminalia, ventral view. 51, Male terminalia, dorsal view. 52, Male terminalia (phallic structures), dorsal view. Scale bars = 0.5 mm (Figs. 48–49), 0.1 mm (Figs. 50–52).



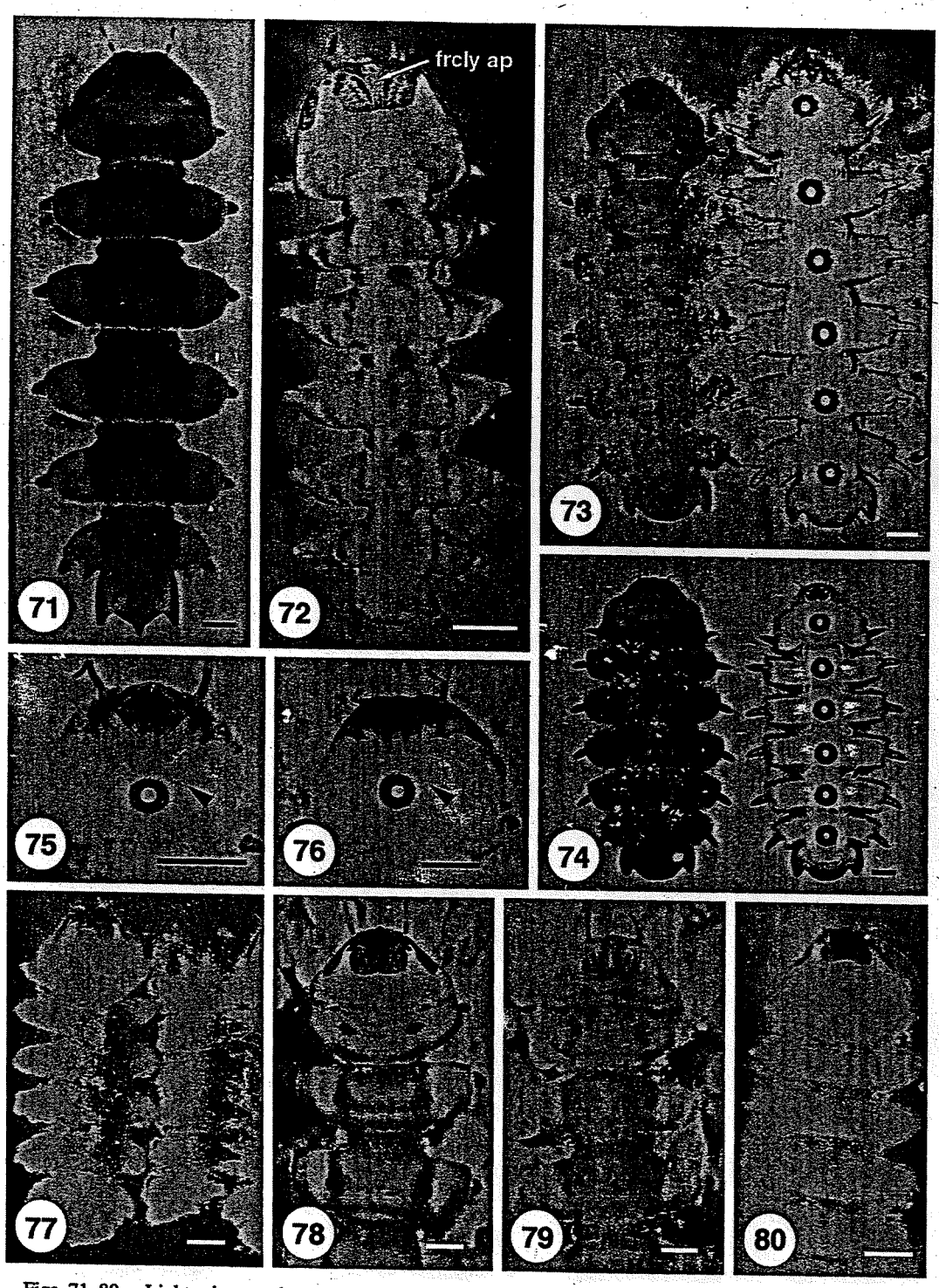
Figs. 53–58. Male terminalia of *Blepharicera*, dorsal views. 53, *B. appalachiae*. 54, *B. cherokea*. 55, *B. coweetae*. 56, *B. diminutiva*. 57, *B. tenuipes*. 58, *B. williamsae*. Scale bars = 0.25 mm. (all after Hogue 1987).



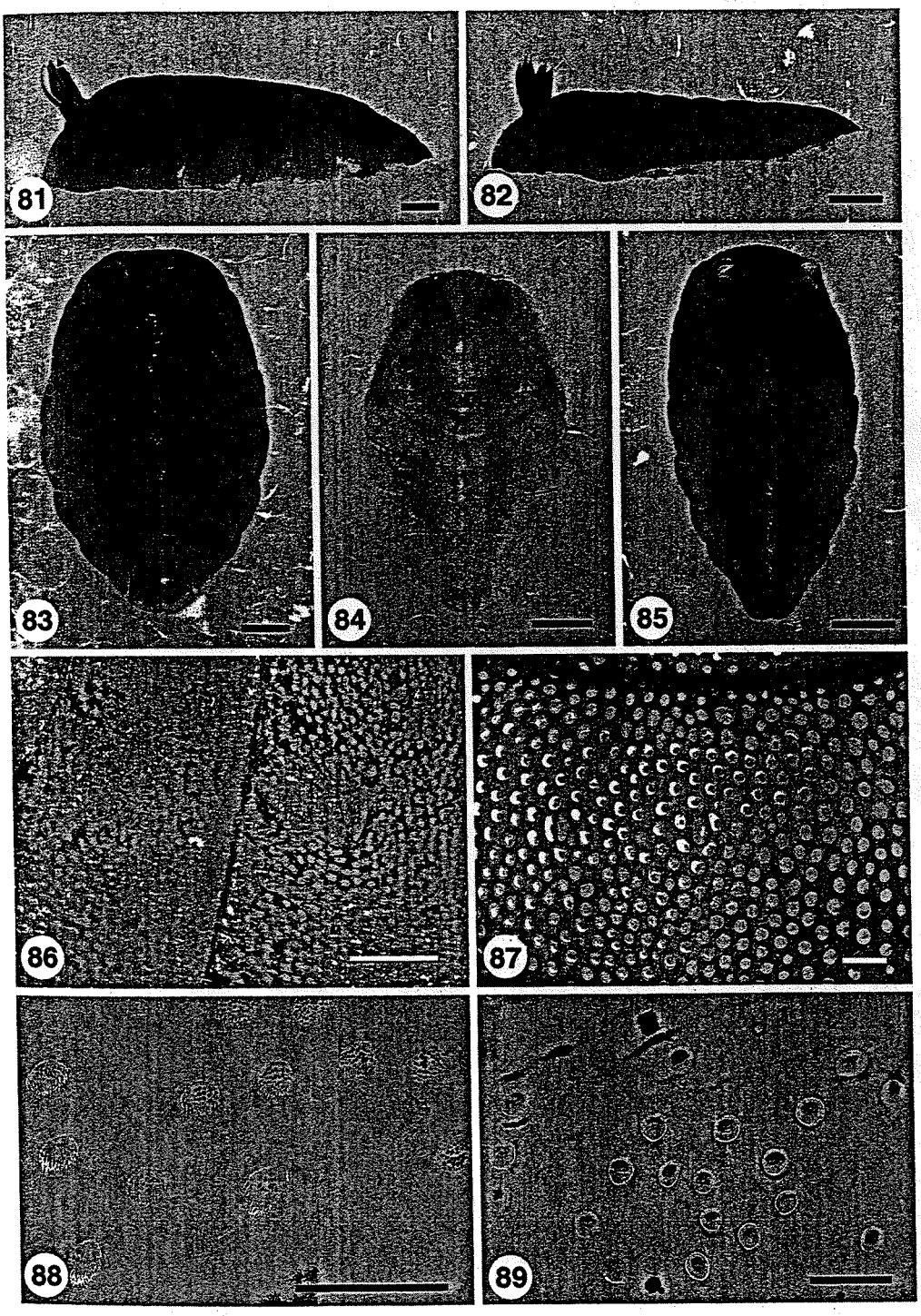
Figs. 59–64. Male terminalia (phallic structures) of *Blepharicera*, dorsal views. 59, *B. appalachiae*. 60, *B. cherokea*. 61, *B. coweetae*. 62, *B. diminutiva*. 63, *B. tenuipes*. 64, *B. williamsae*. Scale bars = 0.25 mm. (59–61 modified from Hogue 1987, 62–64 after Hogue 1987).



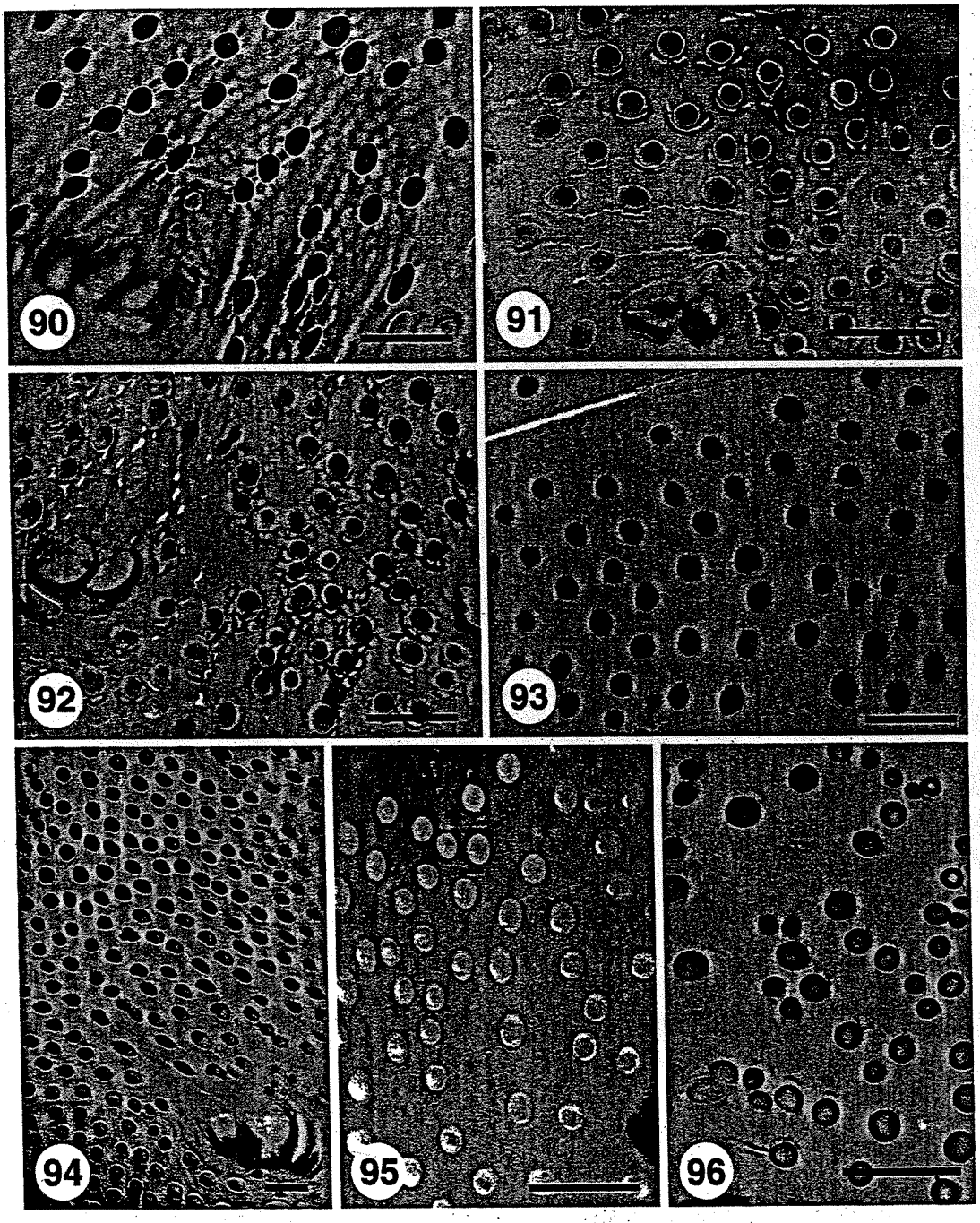
Figs. 65–70. Terminalia of *Blepharicera*. 65, Male terminalia of *B. capitata*, dorsal view. 66, Male terminalia (phallic structures) of *B. capitata*, dorsal view. 67, Male terminalia of *B. similans*, dorsal view. 68, Male terminalia (phallic structures) of *B. similans*, dorsal views. 69, Female terminalia of *B. capitata*, ventral view. 70, Female terminalia of *B. similans*, ventral view. Scale bars = 0.25 mm. (all after Hogue 1987).



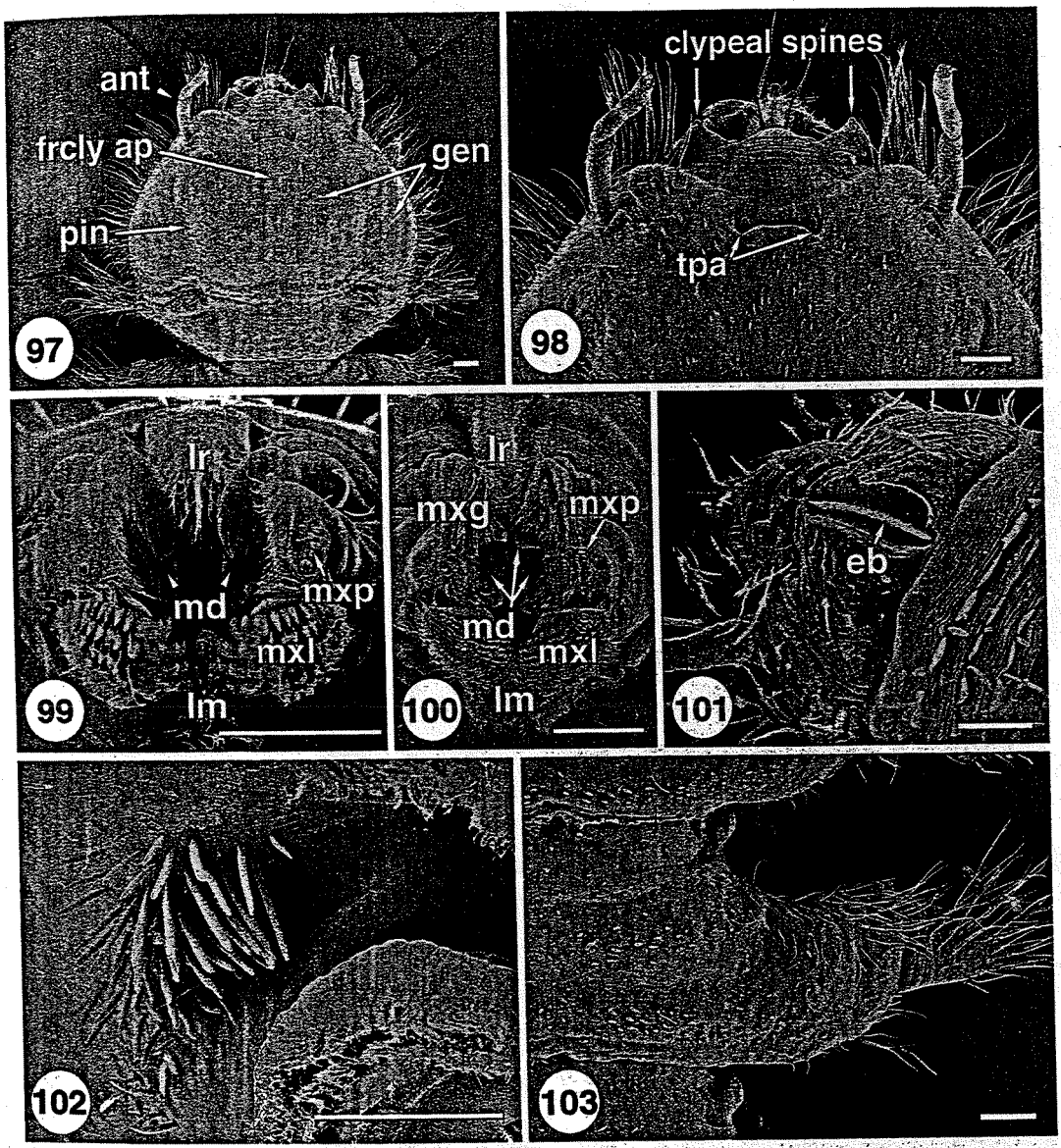
Figs. 71–80. Light micrographs of larval *Blepharicera*. 71, *B. caudata*, dorsal view. 72, *B. chattooga*, dorsal view (frcly ap = frontoclypeal apotome). 73, *B. magna* (fall morphotype), dorsal (left) and ventral (right) view. 74, *B. magna* (spring morphotype), dorsal (left) and ventral (right) view. 75, *B. diminutiva*, ventral view showing substernal sensilla (arrow). 76, *B. williamsae*, ventral view showing substernal sensilla (arrow). 77, *B. separata*, dorsal (left) and lateral (right) view. 78, *B. williamsae*, dorsal view. 79, *B. coweetae*, dorsal view. 80, *B. capitata*, dorsal view. Scale bars = 0.5 mm.



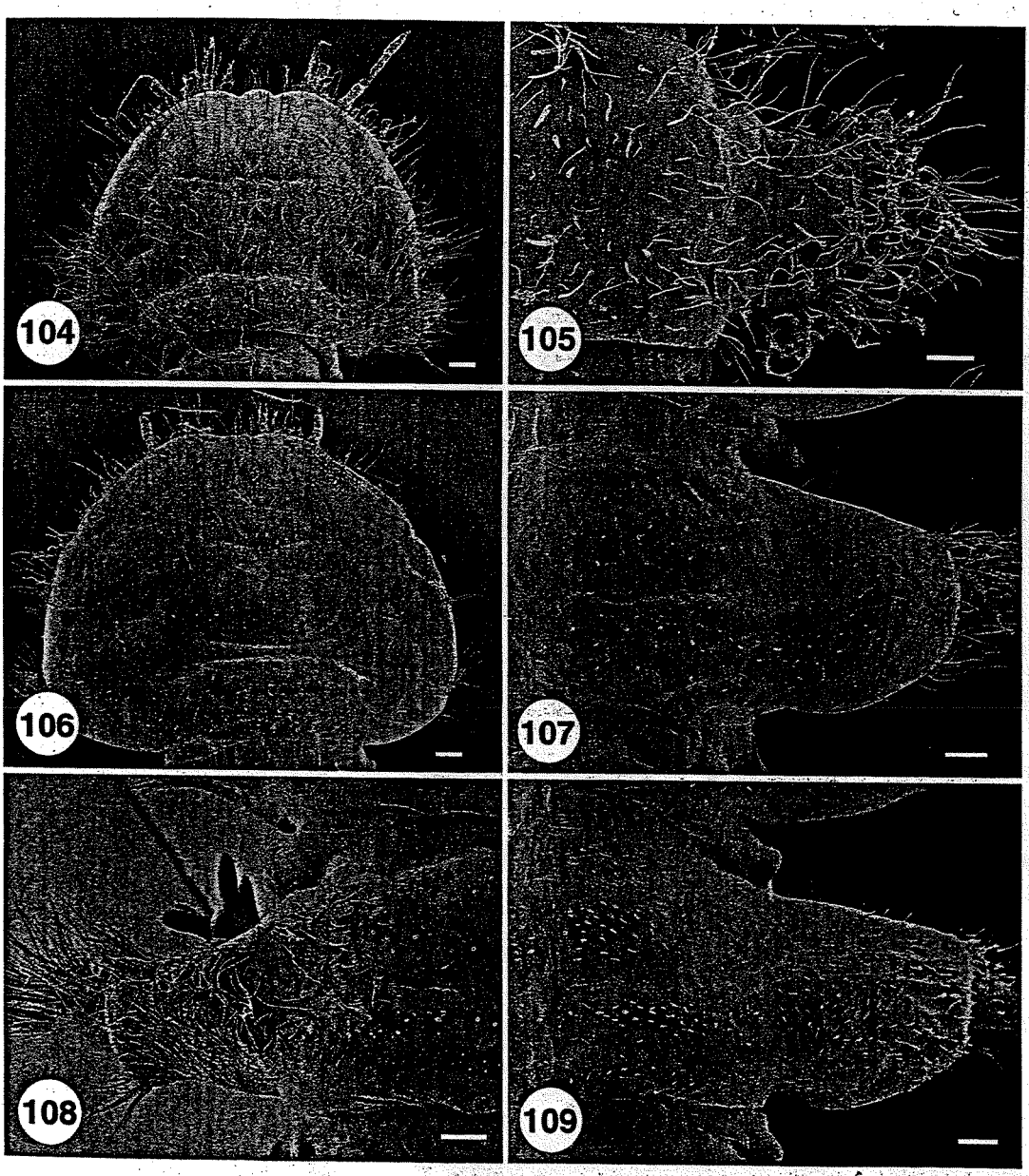
Figs. 81–89. Light micrographs of pupal *Blepharicera*. 81, *B. williamsae*, lateral view. 82, *B. appalachiae*, lateral view. 83, *B. appalachiae*, dorsal view. 84, *B. separata*, dorsal view. 85, *B. diminutiva*, dorsal view. 86, *B. gelida* microsculpture, abdominal tergites III-IV (reflected light). 87, *B. gelida* microsculpture, abdominal tergite V (transmitted light). 88, *B. cherokea* microsculpture, abdominal tergite III. 89, *B. corniculata* microsculpture, abdominal tergite IV. Scale bars = 50 μm (Figs. 87–89), 0.2 mm (Fig. 86), 0.5 mm (Figs. 81–85).



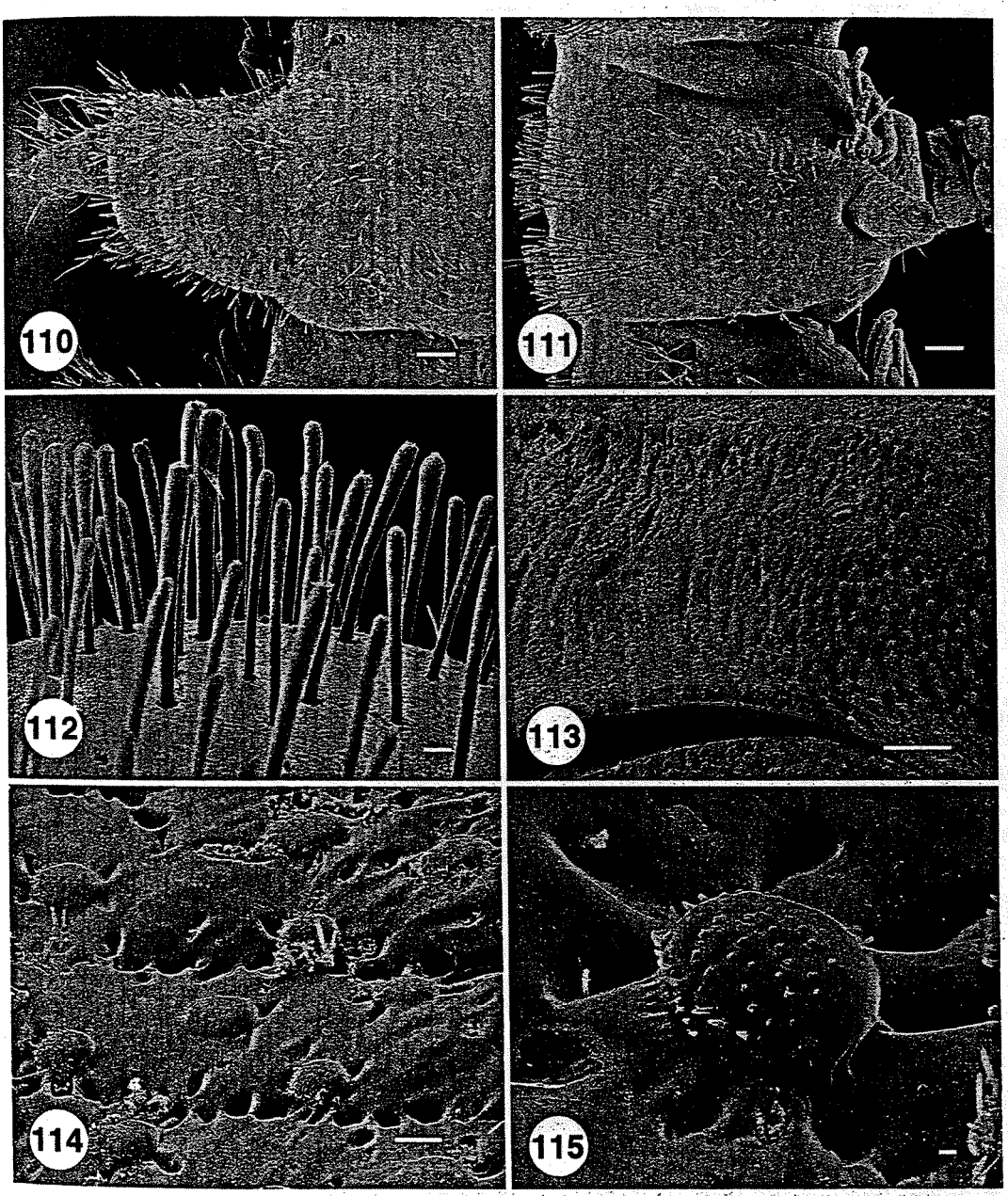
Figs. 90–96. Light micrographs of pupal *Blepharicera*, microsculpture on abdominal tergites. 90, *B. tenuipes*. 91, *B. coweetae*. 92, *B. hispida*. 93, *B. chattooga*. 94, *B. magna*. 95, *B. capitata*. 96, *B. appalachiae*. Scale bars = 50 μm.



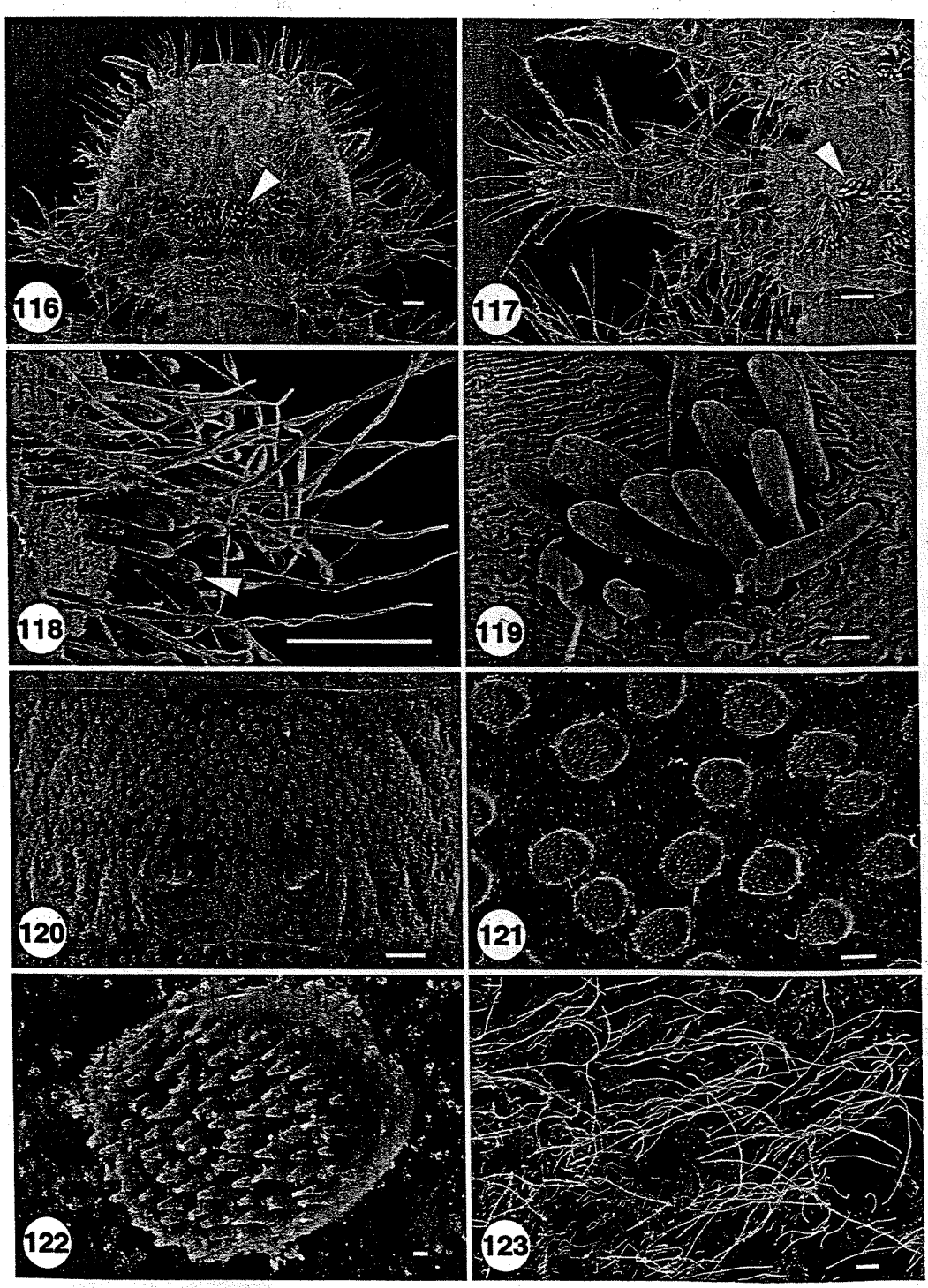
Figs. 97–103. Scanning electron micrographs of larval Blephariceridae. 97, *Blepharicera corniculata* cephalothorax. 98, *B. corniculata,* anterior margin of cranium showing clypeal spines. 99, *Bibiocephala grandis* instar I mouthparts. 100, *B. cherokea* mouthparts. 101, *Agathon comstocki* instar I head capsule, oblique-dorsal view of egg burster. 102, *B. diminutiva,* substernal sensilla. 103, *B. corniculata,* abdominal segment III, dorsal view of right side. Scale bars = 100 μm. (abbreviations: ant = antenna; eb = egg burster; frcly ap = frontoclypeal apotome; gen = gena; lm = labium; lr = labrum; md = mandible; mxc = cardo; mxg = galea; mxl = lacinia; mxp = maxillary palpus; pin = posterior cranial excision; tpa = anterior tentorial pits).



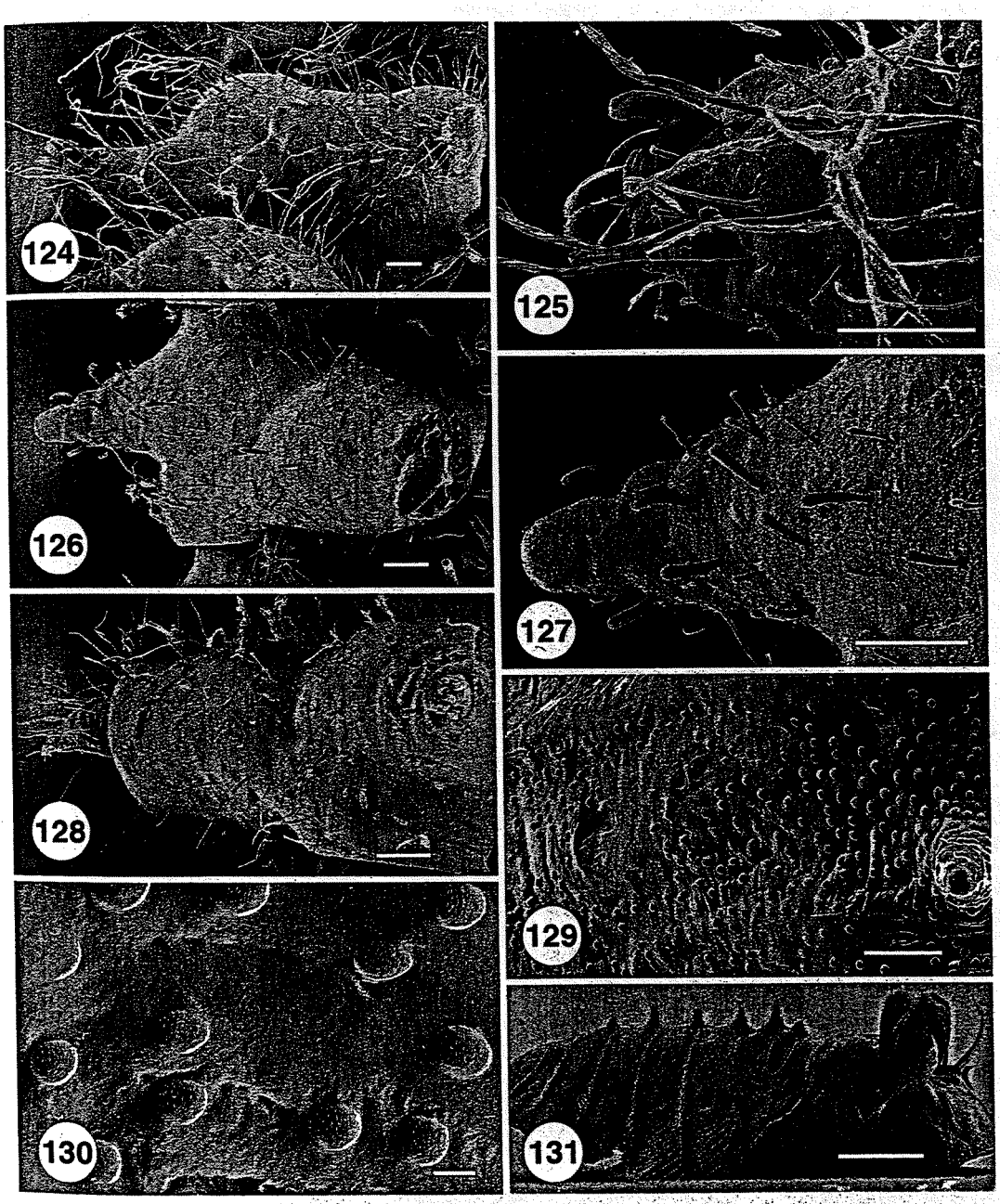
Figs. 104–109. Scanning electron micrographs of larval *Blepharicera*, dorsal views. 104, *B. appalachiae* cephalothorax. 105, *B. appalachiae* abdominal segment III, dorsal view of right side. 106, *B. cherokea* cephalothorax. 107, *B. cherokea* abdominal segment III, right side. 108, *B. diminutiva* abdominal segment III, left side. 109, *B. coweetae* abdominal segment III, right side. Scale bars = 100 μm.



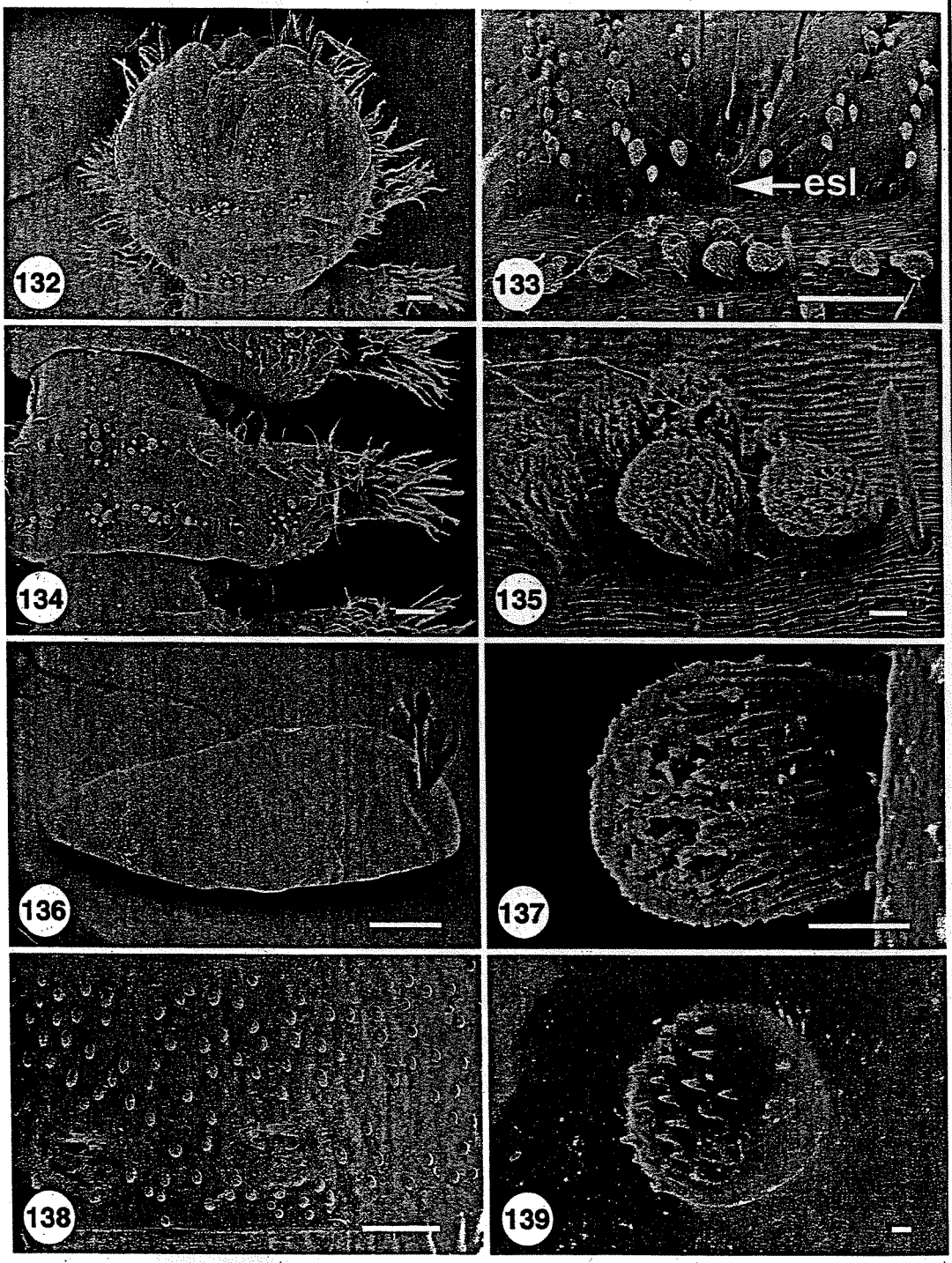
Figs. 110–115. Scanning electron micrographs of *B. hispida*. 110, Larval abdominal segment IV, dorsal view of left side. 111, Larval abdominal segment III, lateral view of right side. 112, Sensilla on larval abdominal segment III. 113–115, Pupal microsculpture, abdominal tergites. Scale bars = 1 μm (Fig. 115), 10 μm (Figs. 112, 114), 100 μm (Figs. 110–111, 113).



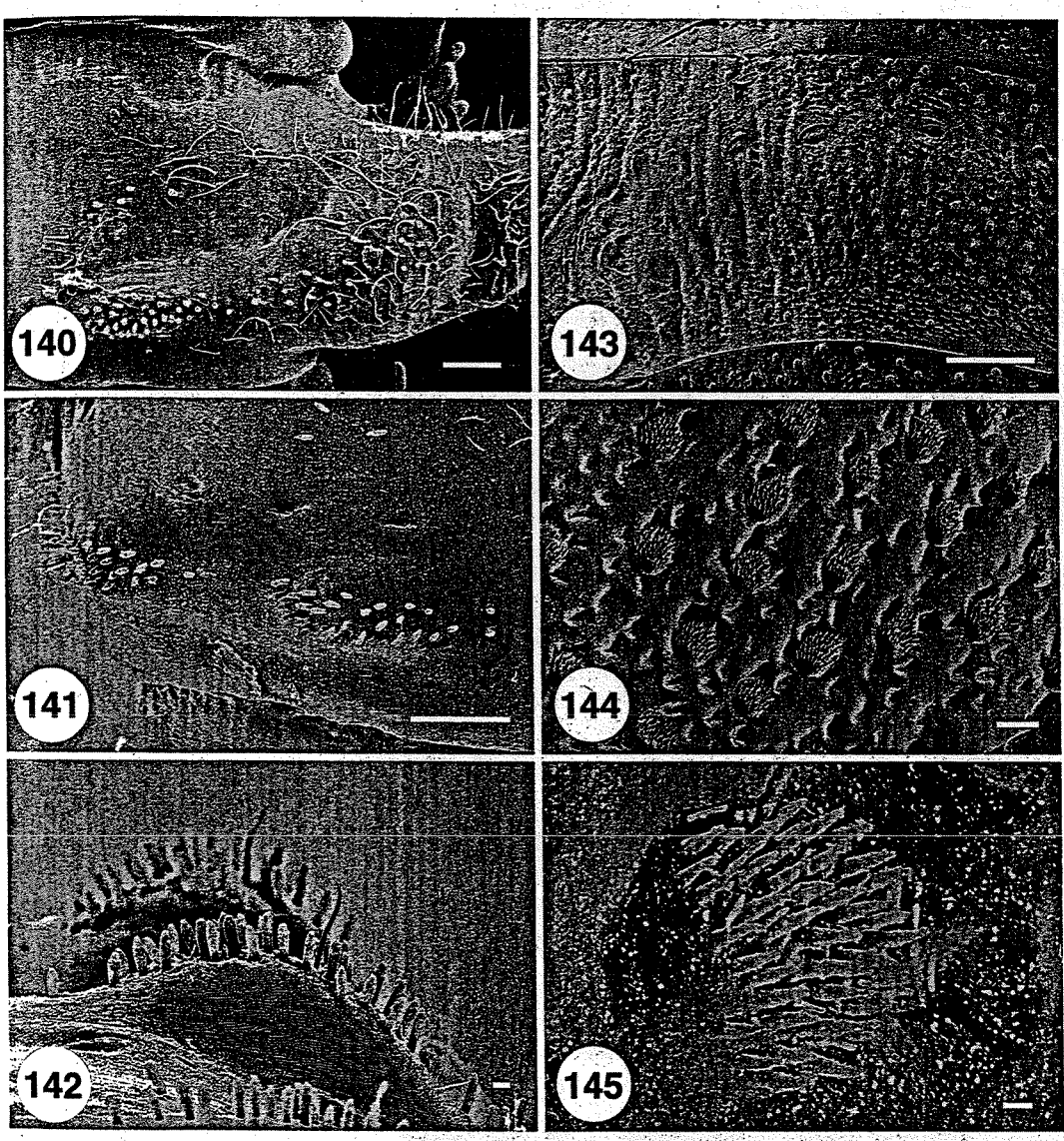
Figs. 116–123. Scanning electron micrographs of *B. magna*. 116, Cephalothorax of fourth-instar larva (fall morphotype). 117, Larval abdominal segment IV (fall morphotype), dorsal view of left side. 118, Digitiform and taeniaform sensilla on larval abdominal segment IV. 119, Digitiform sensilla, larval abdominal segment IV. 120–122, Pupal microsculpture near midline, abdominal tergite V. 123, Pupal microsculpture near lateral margin, abdominal tergite VI. Scale bars = 1 μm (Fig. 122), 10 μm (Figs. 119, 121, 123), 100 μm (Figs. 116–118, 120).



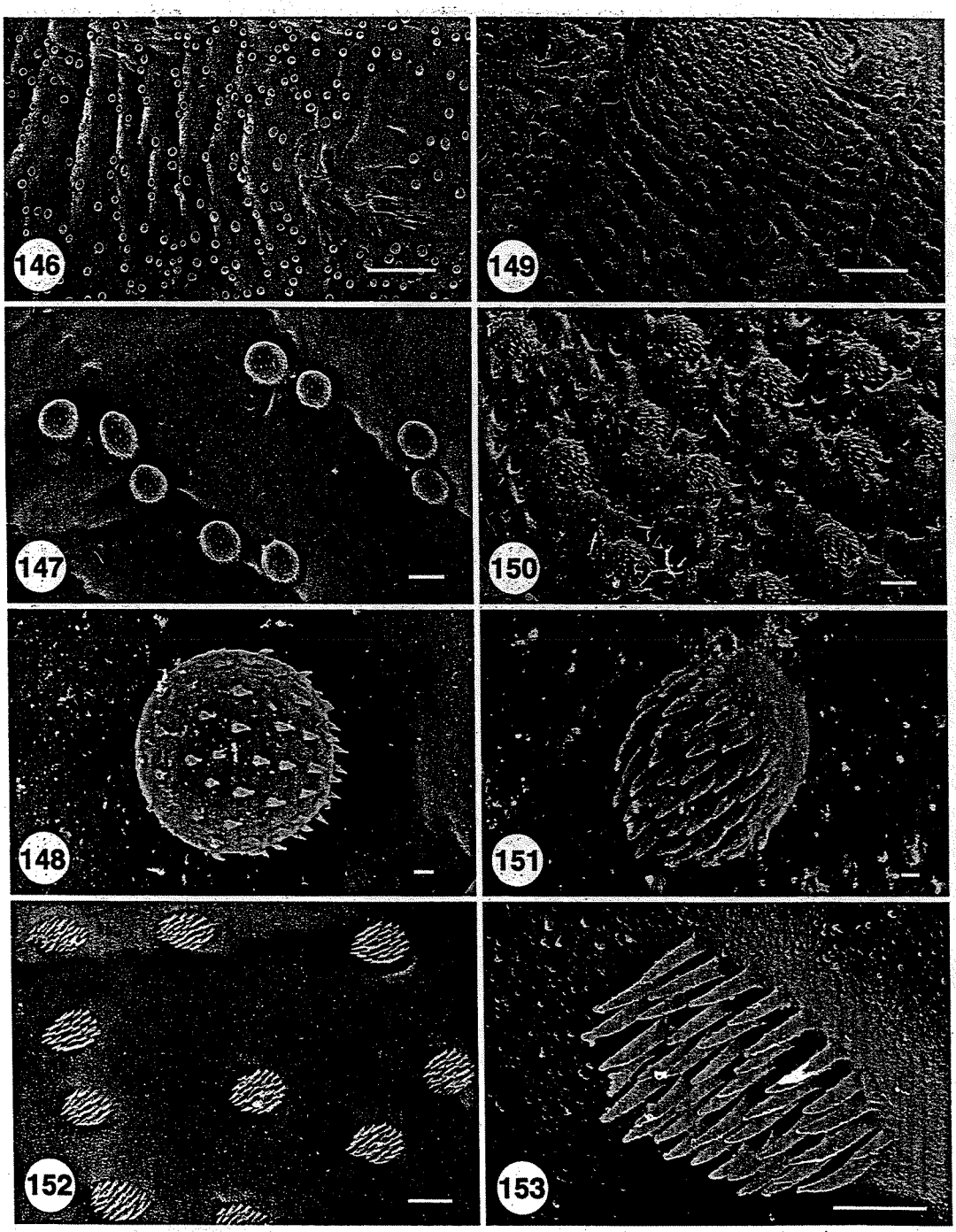
Figs. 124–131. Scanning electron micrographs of *B. capitata* (Figs. 124–125) and *B. separata* (Figs. 126–131). 124, Larval abdominal segment V, lateral view of right side. 125, Apex of dorsal tubercle, larval abdominal segment V, lateral view. 126, Larval abdominal segment IV, lateral view of right side. 127, Apex of dorsal tubercle, larval abdominal segment IV, lateral view. 128, Larval abdominal segment IV, dorsal view. 129, 130, Pupal microsculpture, abdominal tergite IV. 131, Habitus lateral view of pupa. Scale bars = 10 μm (Fig. 130), 100 μm (Figs. 124–129), 0.5 mm (Fig. 131).



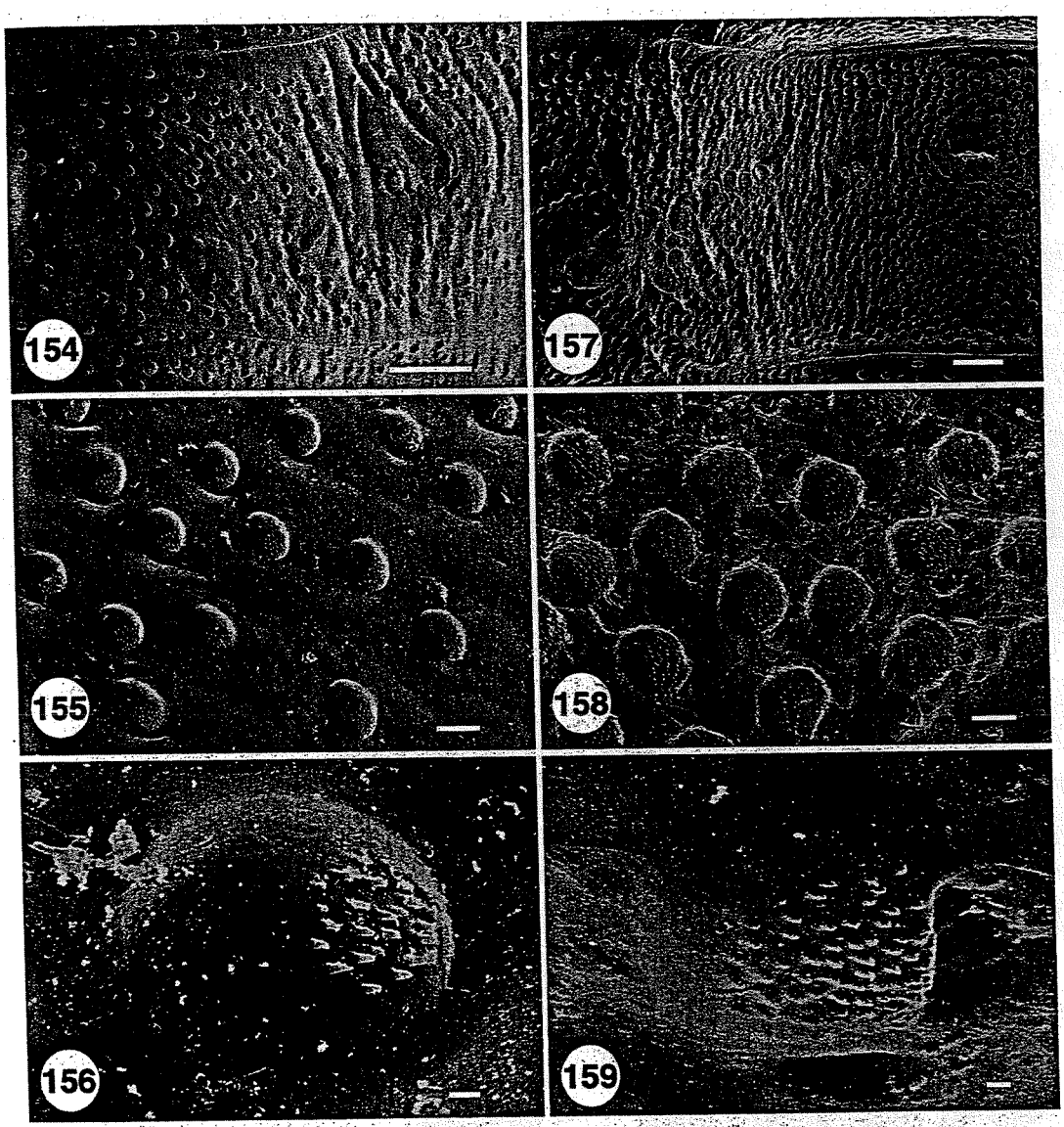
Figs. 132–139. Scanning electron micrographs of *B. similans*. 132, Larval cephalothorax. 133, Larval cranium near posterior margin (esl = ecdysial stem line). 134, Larval abdominal segment III, dorsal view of right side. 135, Cluster of globose sensilla, larval abdominal segment IV. 136, Habitus lateral view of pupa. 137, Globose sensillum, larval abdominal segment IV. 138, 139, Pupal microsculpture, abdominal tergite III. Scale bars = 1 μm (Fig. 139), 10 μm (Figs. 135, 137), 100 μm (Figs. 132–134, 138), 0.5 mm (Fig. 136).



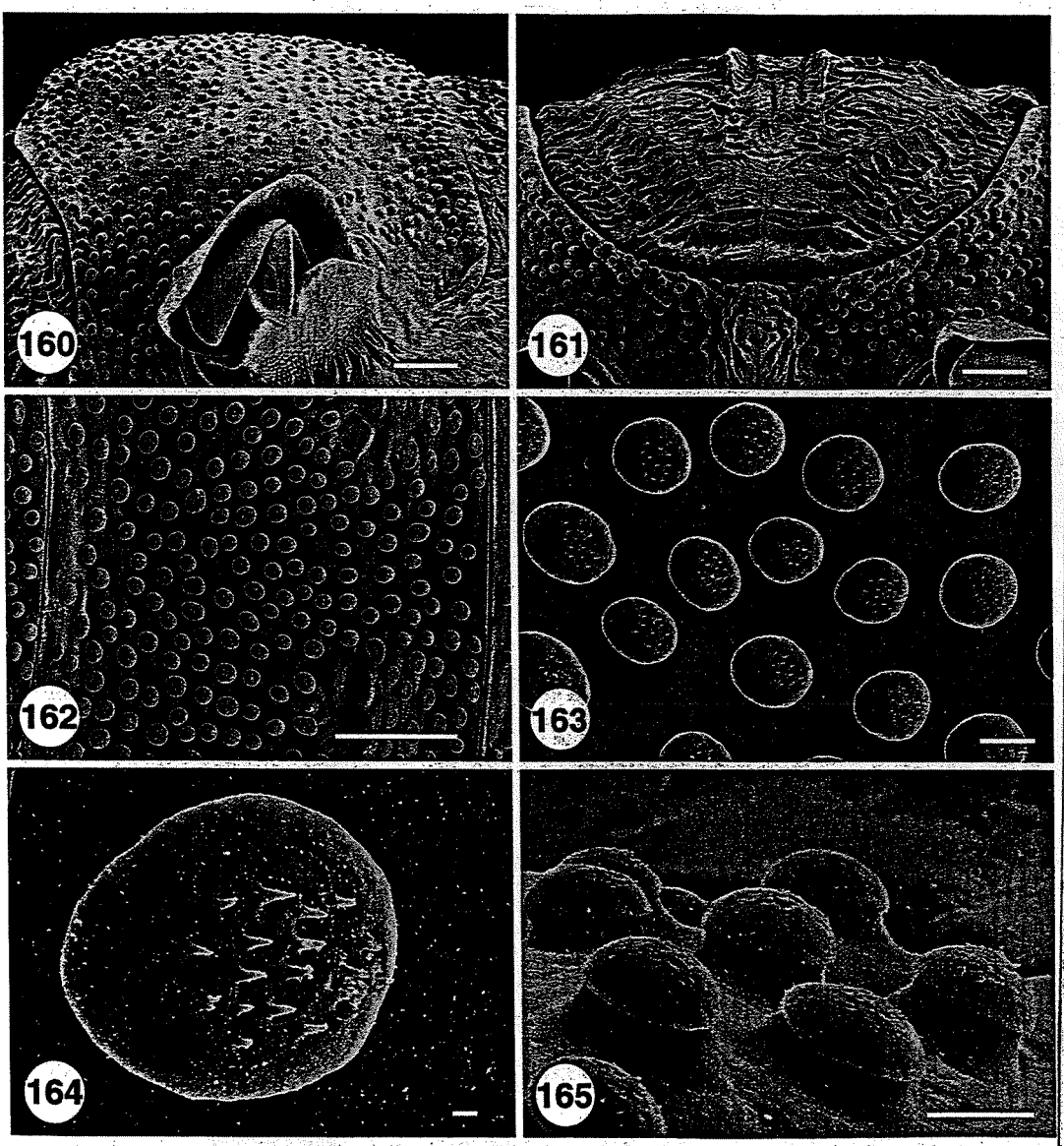
Figs. 140–145. Scanning electron micrographs of *B. tuberosa*. 140, Larval abdominal segment III, dorsal view of right side. 141, Dorsal tubercles on larval abdominal segment IV, oblique-dorsal view. 142, Dorsal tubercles on larval abdominal segment IV, frontal view. 143–145, Pupal microsculpture, abdominal tergite IV. Scale bars = 1 μm (Fig. 145), 10 μm (Figs. 142, 144), 100 μm (Figs. 140, 141, 143).



Figs. 146–153. Scanning electron micrographs of pupal *Blepharicera*, abdominal microsculpture. 146–148, *B. appalachiae*, tergite IV. 149–151, *B. coweetae*, tergite III. 152–153, *B. cherokea*, tergite II. Scale bars = 1 μm (Figs. 148, 151), 4 μm (Fig. 153), 10 μm (Figs. 147, 150, 152), 100 μm (Figs. 146, 149).



Figs. 154–159. Scanning electron micrographs of pupal *Blepharicera*, abdominal microsculpture of tergite IV. 154–156, *B. chattooga*. 157–159, *B. gelida*. Scale bars = 1 μm (Figs. 156, 159), 10 μm (Figs. 155, 158), 100 μm (Figs. 154, 157).



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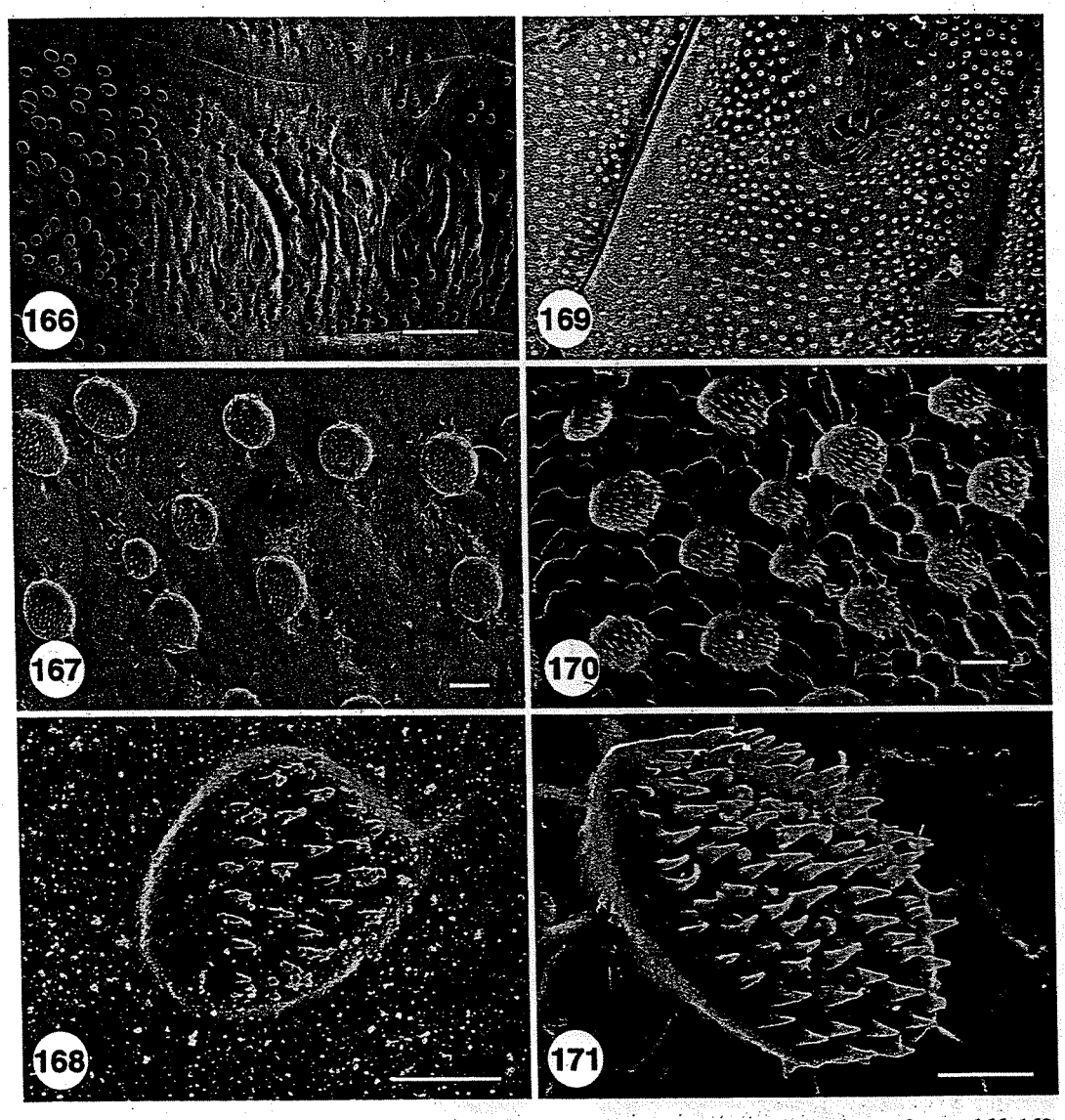

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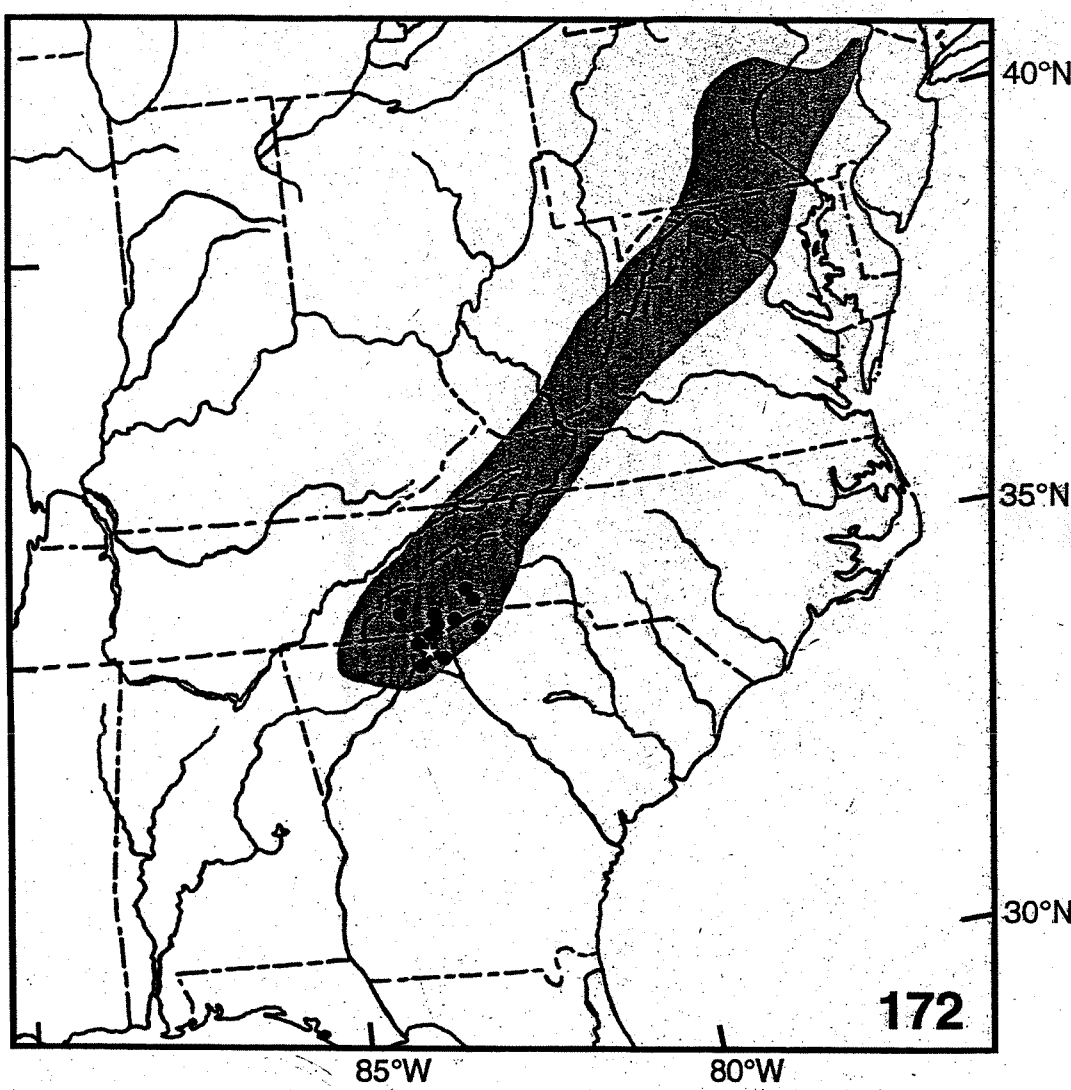


Fig. 172. Distribution of *Blepharicera appalachiae* (shaded area), *B. diminutiva* (●), *B. chattooga* and *B. corniculata* (✪ [= Chatooga River]).

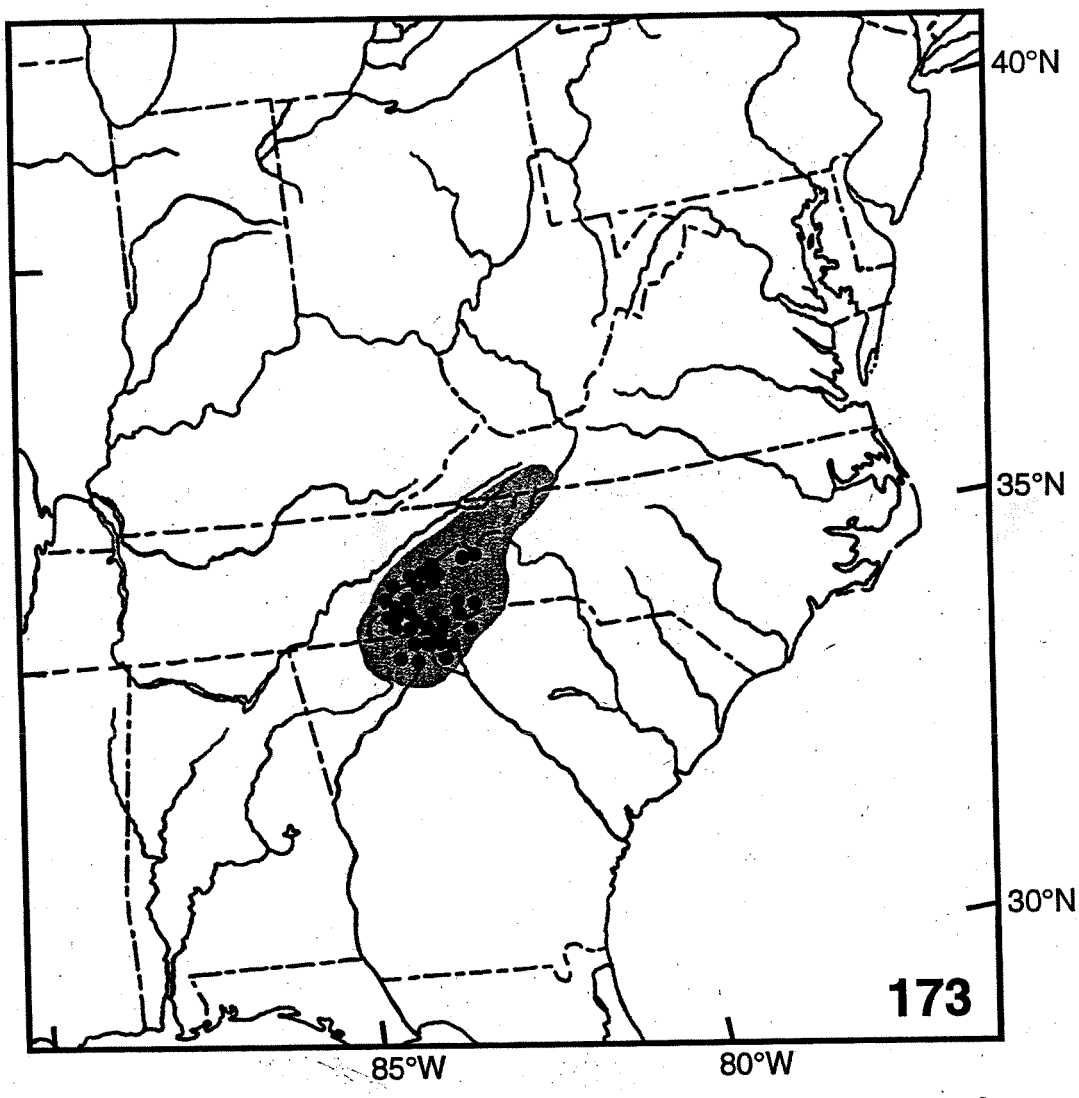


Fig. 173. Distribution of *Blepharicera coweetae* and *B. williamsae* (shaded area), *B. cherokea* (●).

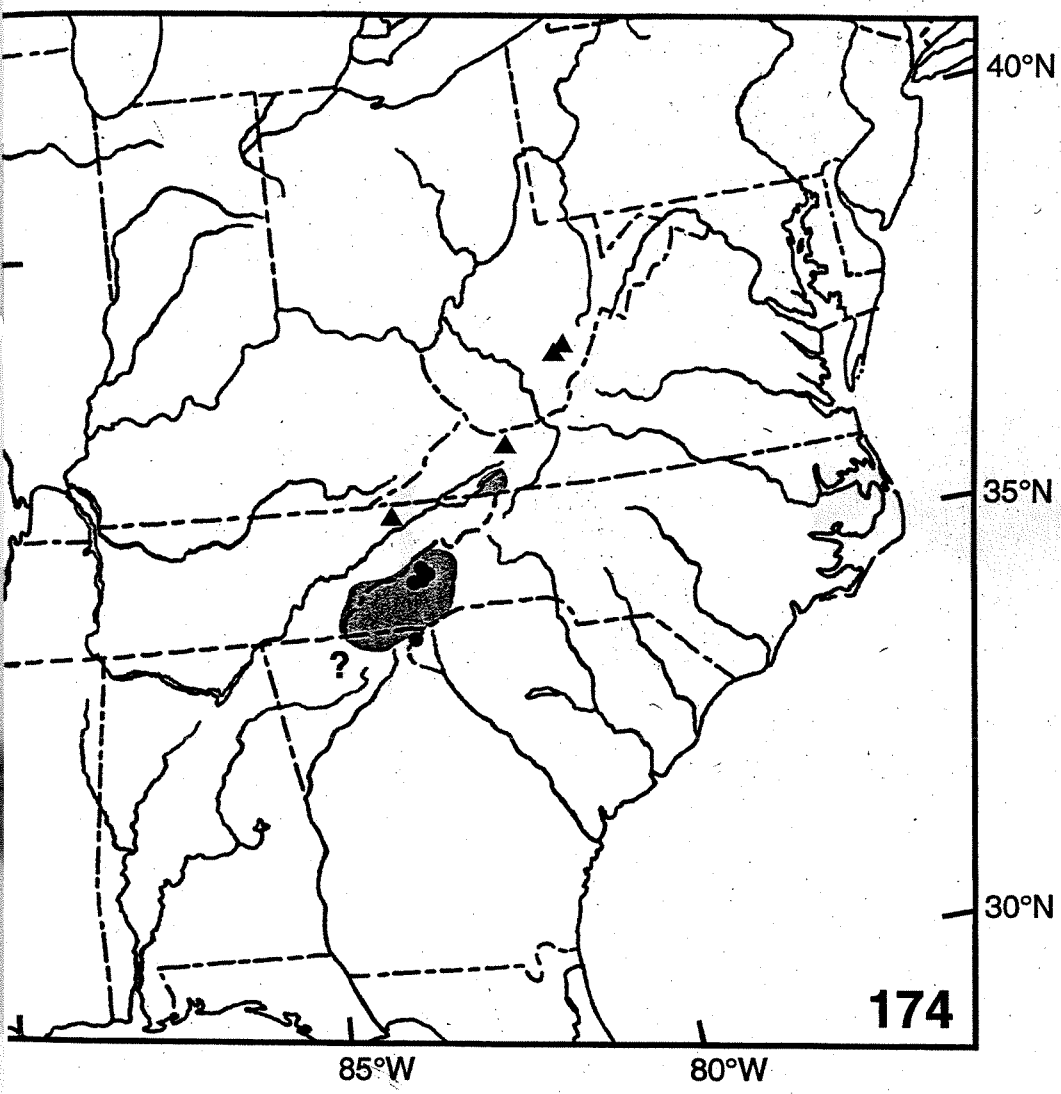


Fig. 174. Distribution of *Blepharicera gelida* (▲), *B. magna* (●), *B tuberosa* (shaded area).

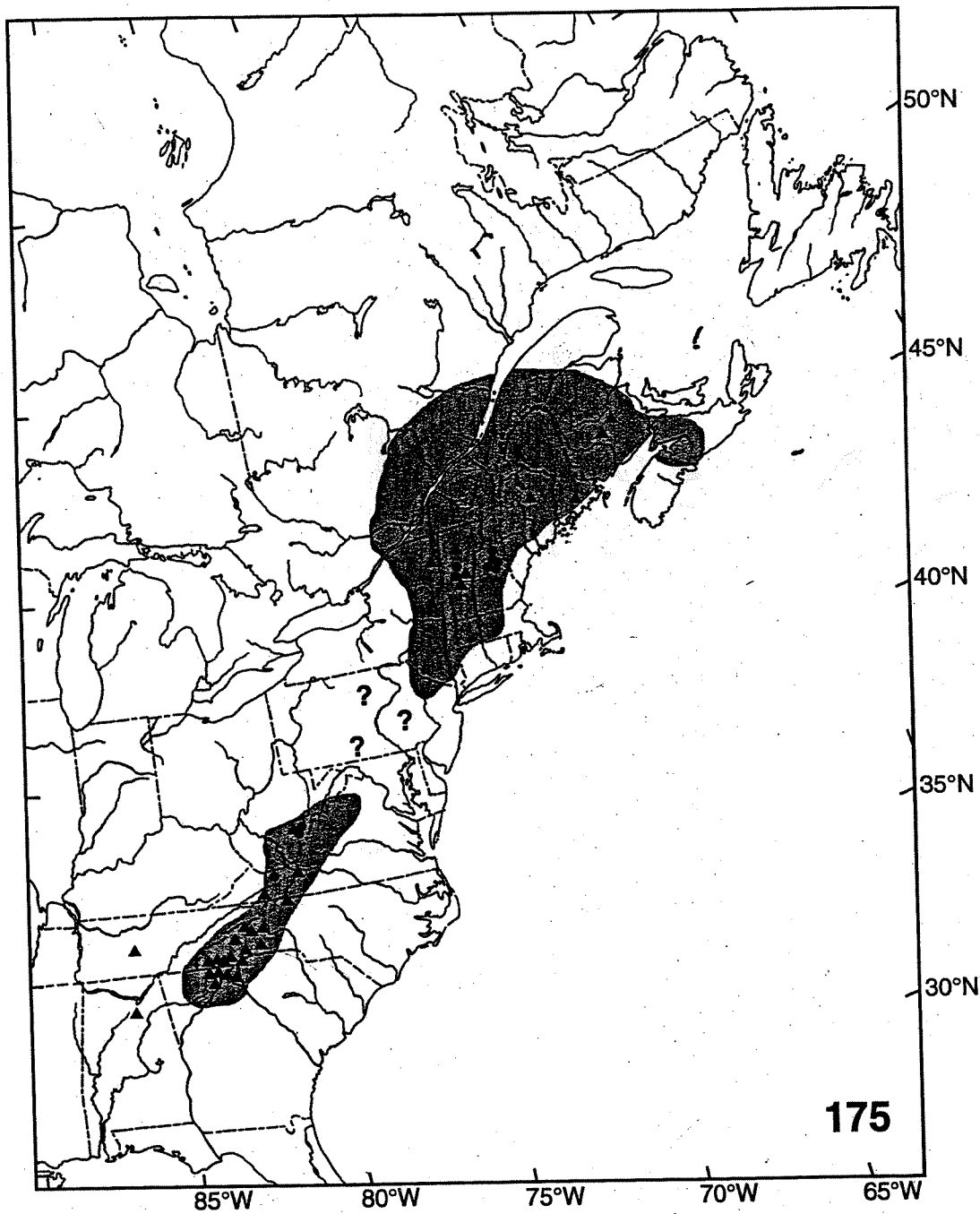
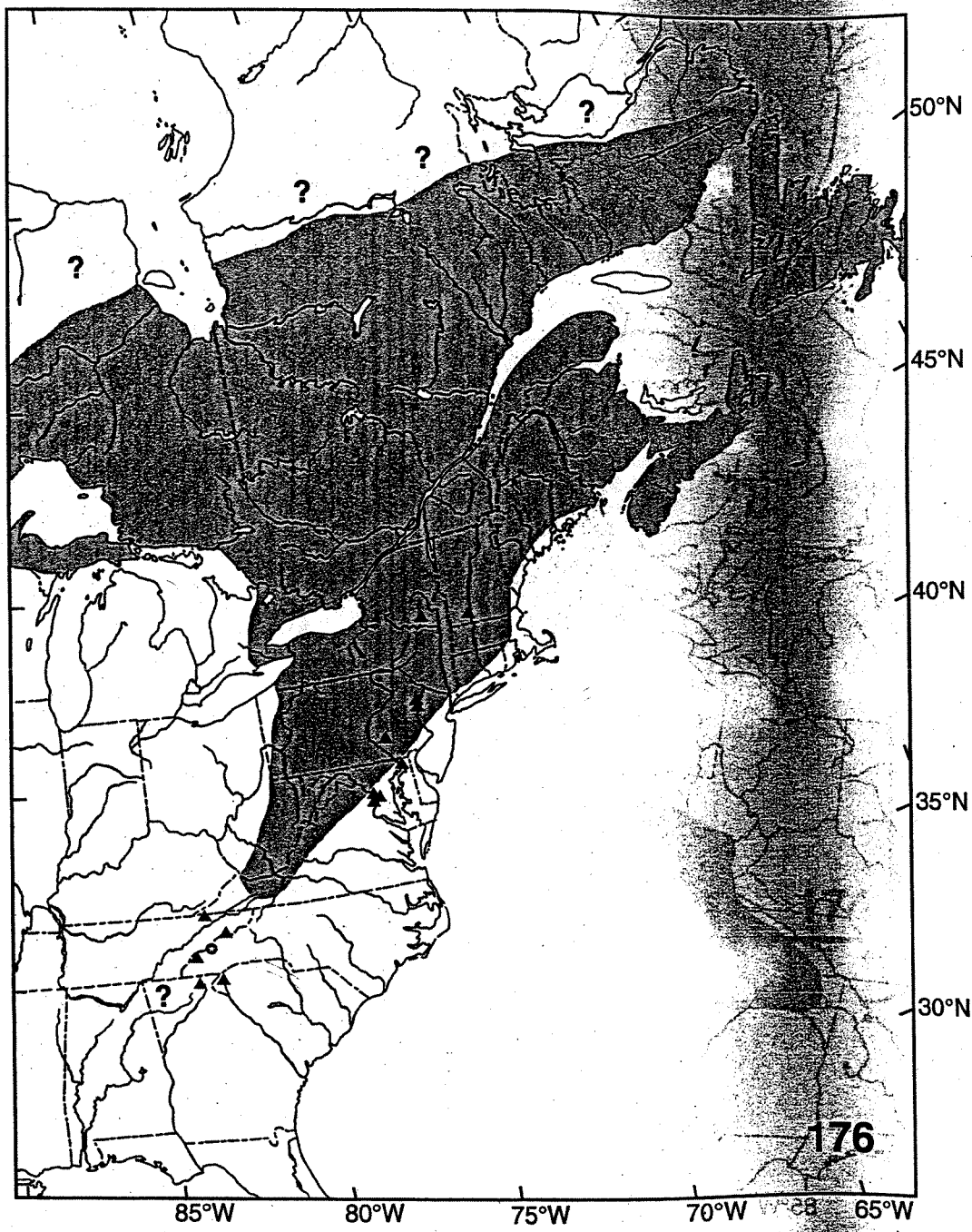


Fig. 175. Distribution of *Blepharicera hispida* (●), *B. separata* (▲), *B. similans* (shaded area).



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