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A Revision of the Genus *Caenis* in North America (Ephemeroptera: Caenidae)¹

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ABSTRACT

The North American species of the genus *Caenis* are revised, and illustrated keys to larvae and adults presented. Eleven nominal species, including one new species, are recognized. Based on shared morphological and behavioral characters in the larvae, adults, and eggs, these species are grouped as follows: diminuta group - *C. amica* Hagen, *C. candida* Harper and harper, *C. diminuta* Walker, *C. latipennis* Banks, *C. punctata* McDunnough, and *C. youngi* Roemhild; hilaris group - *C. anceps* Traver, *C. hilaris* Say, *C. macafferti* n. sp., and *C. tardata* McDunnough. *Caenis bajaensis* Allen and Murvosh appears to have been independently derived and is not placed in either group. For each nominal species, synonymies, larval and adult descriptions, figures, and a discussion of taxonomy, distribution, and biology and ecology, are included. Newly discovered synonyms are: *C. amica* Hagen = *C. simulans* McDunnough n. syn.; *C. latipennis* Banks = *C. forcipata* McDunnough n. syn., *C. jocosa* McDunnough n. syn., *C. delicata* Traver n. syn., *C. gigas* Burks n. syn. [Key words: *Caenis*, Caenidae, mayflies, classification, revision].

Introduction

The mayfly family Caenidae is widely distributed throughout the world, except for most oceanic islands. Larvae occur in a broad range of both lotic and lentic habitats. Although among the smallest mayflies, they often occur in very large numbers and emergences may rival those of some of the largest mayflies such as *Hexagenia* and *Ephoron*.

Of the 13 presently recognized genera of Caenidae, only Caenis Stephens, Brachycercus Curtis, Amercaenis Provonsha and McCafferty, and Cercobrachys Soldan are known to occur in North America. Amercaenis was recently erected to accommodate the species previously known as Caenis ridens McDunnough, the larva of which is one of the most unique among the Caenidae (Provonsha and McCafferty, 1985). Soldan (1986) established Cercobrachys in his revision of the Caenidae with ocellar tubercles in the larval stage.

Caenis hilaris (Say), 1839, was the first North American species of the genus to be

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described. Subsequently, *C. diminuta* Walker, 1853, *C. amica* Hagen, 1861, and *C. latipennis* Banks, 1907, were described. McDunnough (1931) comprehensively treated the North American Species, redescribed and keyed the adults of the above species and added *C. forcipata* McDunnough, *C. ridens* McDunnough, *C. punctata* McDunnough, *C. tardata* McDunnough, *C. jocosa* McDunnough, and *C. simulans* McDunnough. Traver (1935) also described and keyed all known species and added *C. anceps* Traver and *C. delicata* Traver. Burks (1953) described and keyed those species known from Illinois and added *C. gigas* Burks. Thew (1960) revised the genera of Caenidae known at that time and provided much information on North American *Caenis*. Recently, *C. candida* Harper and Harper, 1981, was described on the basis of adults; *C.bajaensis* Allen and Murvosh, 1983, was described from larvae only; and *C. youngi* Roemhild, 1984, was described on the basis of adults and larvae.

Although the larvae of most European *Caenis* species have been known for some time (Grandi, 1942, 1966; Macan, 1955, 1979; Malzacher, 1976, 1984; Müller-Liebenau, 1958), only the larvae of *C. bajaensis* and *C. youngi* have been described from North America.

Smith (1935) described and figured the eggs of several north American species of *Caenis*. He was unsure of his female identifications and some were in error. Koss (1968, 1969) described, figured and keyed several North American *Caenis* eggs. Information on the eggs of European species has been given by Degrange (1960), and more recently by Malzacher (1982) who presented a very detailed study of the eggs of European Caenidae and included many SEM photographs.

Edmunds et al. (1976) stated, "although the species of this genus are difficult to separate, the adults should be identifiable with the existing keys." This statement was accurate on both counts. Historically, the adults of *Caenis* have been difficult to separate and the examination of numerous collections revealed that few workers have been in total agreement on their identifications. The keys prepared by McDunnough (1931), Traver (1935), and Burks (1953) did work reasonably well for species concepts as understood at the time they were written. The recent discovery of additional species and the synonymy herein of others, however, has made these earlier keys much less applicable.

The research of North American *Caenis* was undertaken to revise species concepts that would account for population and individual variability, and to provide comprehensive, illustrated descriptions and usable keys for the identification of both adults and larvae.

METHODS AND MATERIALS

During this study, over 26,000 specimens of *Caenis* were examined. Morphological and color pattern variability in specimen series from throughout the temporal as well as the geographic ranges of the genus were catalogued, analyzed, and compared with type material. Comparisons were also made with all European species and as many South American species (both identified and unidentified) as could be obtained. With the exception of *C. youngi*, reared material was the basis of establishing specific larval associations. Biological data, such as larval habitat preferences and attachment-thread deployment strategies in eggs, were also used to understand species and species groups.

Keys were designed to be utilitarian and do not necessarily reflect phylogenetic relationships. Although the larva of *Amercaenis* is distinct, no generic characters have been found that will consistently separate the adults from *Caenis*. *Amercaenis* is therefore included in the adult *Caenis* key.

Distribution maps include only those localities verified during this study. Each species

account also contains an abbreviated list of material examined. The selected entries are representative of the temporal and geographical distribution of each species and are not a full accounting of all specimens examined during this study. A complete list is available from the author.

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CHARACTERS AND TERMINOLOGY

The caenids possess a number of unique character states among mayflies. Species characters requiring clarification or an explanation of terminology are discussed below.

LARVA: Mouthpart differences are of identification value on the generic level and although there are some differences between species of *Caenis*, which may provide useful phylogenetic information, they have not been used in this study.

Differences in the number, arrangement and shape of leg setae are used extensively for identification purposes at both the group and species level. The dorsal (outside) surface of the forefemur may have randomly scattered, simple setae only (Fig. 9) or may possess an irregular transverse row of spatulate setae in the apical third (Figs. 82, 83). The thickened lateral margins often cause these setae to appear bifurcate under a light microscope (Fig. 16). The relative length of the setal row on the inner (anterior) and outer (posterior) margins of the femora (Figs. 10, 12) is of importance. The inner margin of the tibiae and tarsi are edged with spurs (stout spike-like setae) (Fig. 10). The number of spurs on the tibiae is quite variable, but the number on the tarsi is often useful. The presence or absence of a row of fimbriate spurs (small, flat, lanceolate shaped setae with fringed margins) along the ventral surface of the mid and hind tarsi (Figs. 11, 14, 84) is of great diagnostic value.

All North American species of *Caenis* posses at least some denticulation on the tarsal claws (Figs. 22-31). Both the number and size of the claw denticles are of diagnostic value. Although some workers such as Burks (1953) have noted the presence of these denticles, other workers such as Traver (1935), Thew (1960) and Soldan (1978) apparently overlooked them and erroneously considered the absence of denticles as a generic character for *Caenis*. In general, both setation and claw denticulation is not as well developed on the forelegs as they are on the mid and hind legs. All character states mentioned in the species descriptions are taken from the hind legs unless otherwise noted.

The abdomen possesses a number of structures that are useful in differentiating species. The width of the abdomen (Figs. 40-45) is of value and results in part from the relative development of the lateral projections. Other important characters involve the size and shape of the posteromedian projection on the second abdominal tergum (Figs. 32-37) and the shape of the posterior margin of the 9th sternum (Figs. 40-45). It is often necessary to remove the terminal tergum to see this structure clearly.

Gill 1 (Fig. 46) is filiform and although described by Thew (1960) as being two segmented, what appears to be a basal segment is but an outgrowth of the abdominal cuticle.

The large, subquadrate gill 2 (Figs. 48-53) (referred to as the operculate gill) possess a number of species-specific characters. The size of these gills in relation to overall body size is helpful in some cases. The operculate gills of all *Caenis* species possess a Y-shaped ridge on the dorsal surface. Long setae may be present on both the medial and apical forks of this ridge (Fig. 48) or on the medial fork only (Fig. 49). The texture of the dorsal surface varies considerably from species to species (Figs. 88-91) and is of some diagnostic value. There is

a row of minute palmate setae (referred to by most workers as microtrichia) on the ventral surface of the operculate gills (Figs. 48, 85-87). This row is slightly inward from and parallel to the outer margin of the gill. The size of these setae varies somewhat between the two major groups of *Caenis*.

Setation on the caudal filaments follows one of two basic patterns. There can be whorls of short setae only on every second or third segment, with the setae shorter than the intersegmental distance between them (Fig. 39). Or there can be long lateral setae on every segment, in addition to the short whorls, with these setae much longer than the intersegmental space between them (Fig. 38). Setal patterns are most distinct at midlength of the filaments.

Body length may be useful if mature specimens are used. Lengths (for both larvae and adults) are measured dorsally from the anterior margin of the head to the posterior margin of the 10th abdominal tergum along the midline.

ADULTS: Although as many as 14 different morphological characters may be used to differentiate *Caenis* larvae, very few differentiating morphological characters are usable for distinguishing species in the adult stage.

Both the head and thorax are similar among *Caenis* species. Structures of both, however, are useful as landmarks for locating color patterns of specific significance (for example, the T-shaped epicranial suture). Mesothoracic areas and sutures are labeled in Fig. 57. The names of thoracic areas and sutures has, for the most part, been taken from Grandi (1942), Tsui and Peters (1975), and Matsuda (1976). Other terms are used here for the first time.

Differences in wing venation of *Caenis* are important at the group level. Wing vein ICuA1 can be forked with CuA1 basad of an ICuA1-CuP crossvein (Fig. 58), or vein ICuA1 can be forked with CuA2 adjacent to or just distad of a CuA1-CuP crossvein (Figs. 59, 60). The extent of setation along the wing margin (Figs. 58, 59) is also diagnostic for the two groups.

Caenids have well-developed abdominal pleura that protrude somewhat from the abdomen. McDunnough (1931), Traver (1935) and Burks (1953) referred to color markings on the pleura as spiracular dots or dashes; however, they have no relationship to the spiracles and the term has been avoided in this paper. Many individuals, especially subimagos, retain the vestigial remnants of the lateral abdominal projections. The posteromedian projection on abdominal tergum 2 of the larvae is, in some species, also retained (with some modification) in the winged stages. The size of this projection is directly proportional to the size of this structure on the larvae. Thus, those species with a large larval projection also possess a well-developed thin, fleshy, finger-like projection as winged individuals (Figs. 61, 62). On those species having a relatively small larval projection, the projection may be represented by only a small nub on subimagos and totally absent on adults. This projection, when present, is easily seen in alcohol preserved specimens, but may be difficult to locate on pinned material.

The male penes (Figs. 94-99) are similar for all species. Their soft tissue may become variously distorted, however, causing them to be somewhat variable in appearance. The one-segmented genital forceps are of two distinct types. One form has a heavily sclerotized tip with few or no microspines (Figs. 100-103) and the other has a tip densely covered with long microspines (Figs. 105-111). These forceps characters are of the most value at the group level. McDunnough (1931), Traver (1935), and Burks (1953) attempted to use the length and curvature of the forceps as specific characters. Although for some species these characters are of value, there is sufficient variability to make their use very tenuous when attempting to separate closely related species.

The main secondary sexual characteristics differentiating adult females from adult males are a generally larger body, short forelegs, and short setiferous caudal filaments. Both male

and female subimagos are very similar to adult females in these characteristics. General characters used to differentiate adult males to species also apply to adult females and subimagos. Females and subimagos are therefore not distinguished separately in the key, nor are they described in detail within the species descriptions.

COLOR: Historically, color and color pattern differences have been used as primary differentiating characters. Unfortunately, no previously published works provided comparative illustrations of these patterns. The past high reliance on color pattern alone for species differentiation led to the erroneous recognition of many intraspecific color variants of *Caenis* as species.

Although the use of color is still necessary to distinguish both adults and larvae of the various North American species, color patterns are somewhat variable. As is the case with many other insects, the use of color and especially the use of a single isolated color pattern character, can be dangerous in delineating species (Shapiro, 1980, Hamilton, 1982, McCafferty and Pereira, 1984). Only by using several color characters in combination, backed by the few existing morphological differences, can proper species identifications of *Caenis* adults be insured.

Both adults and larvae of most species have a small black mark on the femora. This mark is located on or near the outside (dorsal) margin near the femoral apex (Figs. 63-68). The shape and size of this spot is important at the species level. Throughout the text, it is referred to as the preapical spot.

EGGS: Mayfly eggs in general often supply additional morphological characters to aid in species identification and may provide clues to phylogenetic relationships (Koss, 1968). Characters of *Caenis* eggs are useful at the group level and are used within the adult key to help separate associated females.

At one or both ends of *Caenis* eggs are a series of sticky thread-like structures used to attach the egg to the substrate when deposited in water (Figs. 113, 120). In the predepositional state, these threads are tightly compacted into what is called a polar cap (Fig. 119). The shape of the caps and the deployment mechanisms of the threads are useful in segregating females with which they are associated into species groups (for details see systematic accounts section). Other egg structures tend to be fairly uniform in all North American species.

ABBREVIATIONS: The following abbreviations are used for the sex and stage of specimens. M - adult male; F - female; S - subimago; L - larva; LCS - larval cast skin.

Materials from the following collections were studied or are mentioned in the text. Abbreviations are given as they are referred to hereafter.

ANSP Academy of Natural Sciences of Philadelphia, Philadelphia

ASU Arkansas State University, State University
BMNH British Museum (Natural History), London
CAS California Academy of Sciences, San Francisco

CEUM Collection Entomologique de l'Université de Montreal, Montreal

CNC Canadian National Collection, Ottawa

CU Cornell University, Ithaca
CUC Clemson University, Clemson
DPC Duke Power Co., Huntersville, NC
FAM Florida A and M University, Tallahassee
INHS Illinois Natural History Survey, Urbana

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA MNB Museum fur Naturkunde de Humboldt-Universitat zu Berlin, Berlin, DDR

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MSU Michigan State University, Lansing MTSU Montana State University, Bozeman

PERC Purdue Entomological Research Collection, West Lafayette, IN
PMNH Peabody Museum of Natural History, Yale University, New Haven, CT

SAU Southern Arkansas University, Magnolia SWRC Stroud Water Research Center, Avondale, PA UCB University of California at Berkley, Berkley

UF University of Florida, Gainesville
UK University of Kansas, Lawrence
UM University of Mississippi, University

UME University of Maine, Orono
UMSP University of Minnesota, St. Paul

UNL University of Nebraska at Lincoln, Lincoln UNO University of Nebraska at Omaha, Omaha US University of Saskatchewan, Saskatoon

USNM National Museum of Natural History Smithsonian Institution (formerly the collections of

the United States National Museum), Washington, DC

UU University of Utah, Salt Lake City
UW University of Windsor, Ontario

VPI Virginia Polytechnic Institute and State University, Blacksburg.

Systematic Accounts and Keys

Family Caenidae

Larvae of the family Caenidae are distinguished by the following combination of characters: Forewing pads pannote in form (Figs. 2-7); hind wing pads absent; gills on abdominal segment 1 filiform, originating from lateral margin of segment (Fig. 46); gills on segment 2 subquadrate, operculate (Figs. 48-53); gills on 3-6 single, with margins fringed and filiform tufts wanting (Fig. 47); median terminal filament well developed.

Larvae most closely resemble those of the family Neoephemeridae but can be differentiated by the lack of hind wing pads in caenids and the presence of filiform tufts on gills 3-6 in neoephemerids. They are also often confused with members of the family Tricorythidae which also have operculate gills. The presence of gills on segment 1 and the subquadrate shape of the operculate gills in caenids will distinguish them from tricorythids, which lack gills on segment 1 and have triangular or ovate operculate gills.

Adults are characterized by the following combination of characters: Eyes of both sexes small and remote (Figs. 69-81); thorax robust with a medionotal membrane (Fig. 57); one pair of broad wings present, with veins MP2 and IMP almost as long as vein MP1 (Fig. 58); male genital forceps (Figs. 100-111) one-segmented; median terminal filament well developed.

Although the larvae have retained many of the primitive characters of the proto-Neoephemeridae lineage (Edmunds et al. 1976), the adults are highly derived. The wing venation, the medioscutal membrane, and the one-segmented male genital forceps separate caenid adults from all other families of Ephemeroptera. Nevertheless, in general form they resemble adults of Tricorythidae and are often misidentified as such. The presence of a medionotal membrane in Caenidae is the simplest means of separation.

KEY TO THE NORTH AMERICAN GENERA OF CAENIDAE

Larvae

- Head with three ocellar tubercles; forelegs distinctly shorter than mid and hind legs; maxillary and labial palpi two-segmente

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- 1'. Head without ocellar tubercules; forelegs subequal in length to mid and hind legs; maxillary and labial palpi three-segmented 3
- 2. Anterior margin of mesosternum prominent, bearing numerous long bristles; spines on abdominal segment 6 strongly bent medially; legs with bristles as long as tibiae *Cercobrachys*
- 2'. Anterior margin of mesosternum flat, without bristles; spines on abdominal segment 6 not bent medially; legs with bristles shorter than tibiae **Brachycercus**
- 3. Inner margin of foretibia and tarsus densely covered with long setae; segment 3 of labial palp twice as long as segment 2, densely covered with long setae; outer margin of operculate gills fringed with short bifurcate setae

 Amercaenis
- 3'. Inner margin of foretibia and tarsus with row of stout spurs (Fig. 9); segment 3 of labial palp subequal in length or shorter than segment 2, with few moderately long spurs and setae; outer margin of operculate gills fringed with long setae (Fig. 48)

 Caenis

Adults

- Prosternum two to three times as long as broad, triangular in shape; forecoxae closely proximal on venter Americaenis and Caenis
- Prosternum half as long as broad, rectangular in shape; fore-coxae widely separated on venter
- Pedicel only slightly longer than scape or equal in length; spines on abdominal segment 6 considerably bent dorsally; eggs spindle-shaped, 4-6 times longer than broad Cercobrachys
- 2'. Pedicel at least 1.5-2.0 times longer than scape; spines on abdominal segment 6 slightly bent dorsally; eggs oval, 2-3 times longer than broad *Brachycercus*

Genus CAENIS Stephens

Caenis Stephens, 1835: 61. Type species: Caenis macrura Stephens, 1835. Oxycyphus Burmeister, 1839: 796 (in part). Ordella Campion, 1923-518.

LARVA: Body length: 2.0-7.0 mm.

Head.—Head capsule without tubercles; labrum broadly emarginate medially; mandibles with lateral margins fringed with long setae; maxillary palp 3-segmented; labial palp 3-segmented, distal segment as short or shorter than segment 2, with few stout spurs and setae.

Thorax.— Shape robust; all legs subequal in size; forecoxae closely proximal ventrally; inner margin of foretibia and tarsus with row of stout spurs on inner margin (Fig. 9).

Abdomen.— Segments moderately flattened dorsoventrally; lateral margins fringed with setae; posterolateral projections prominent on middle segments, not upcurved; tergum 2 with variously produced posteromedian projection; (all Northern American species with row of long, upwardly directed setae along posterior margin of abdominal terga 7 and 8 and greatly reduced posterolateral projections on segment 9). Gills present on segments 1-6; gill 1 (Fig. 46) originating at anterolateral margin of segment, filiform, 3-4 times mid length of abdominal tergum 2, with scattered setae, oriented laterally; gill 2 (Figs. 48-53) originating from posterior margin of segment, operculate, subquadrate, heavily sclerotized, outer margins fringed with long setae, and dorsal surface with Y-shaped ridge; gills 3-6 (Fig. 47, 92, 93) originating from posterior margin of segment, lamellate, margins fringed, oriented medially, dorsal surface with row of fimbriate setae and densely covered with what are presumed to be chloride cells.

ADULT MALE: Body length 2.0-4.5 mm.

Head.— Antennal pedicel twice as long as scape.

Thorax.— Shape robust; prosternum 2-3 times as long as broad, triangular in shape; forecoxae closely proximal ventrally; foreleg approximately 1.8 times length of mid and hind legs.

Abdomen.— Penes lobes membranous, fused; forceps one segmented (Figs. 94-111). Caudal filaments 3-4 times length of body, lacking setae.

ADULT FEMALE: Body length: 2.5-6.2 mm.

Head.— as in male.

Thorax.— Shape robust as in male. Foreleg subequal in length to mid and hind legs.

Abdomen.— Similar to male (except for primary sex organs). Caudal filaments approximately 2/3 length of body, setiferous.

EGGS: The eggs of North American *Caenis* are of two very distinct types with parallel differences found on the adults and larvae.

Type I: (Figs. 112-115) Ovate, usually with 1 polar cap (rarely 2); polar cap hood-like, enveloping approximately 1/4 of egg; entire egg encased in thin membrane; chorion smooth to finely punctate, with single micropyle (Fig. 112) and no sperm guide.

The Type I eggs of *C. hilaris* and *C. anceps* where placed in water and the deployment of the polar caps was observed. It is presumed that other Type I polar caps react similarly. When submerged in water, the encasing membrane begins to dissolve and slough off (Figs. 113, 114), then a multitude of very fine attachment threads of uniform length gradually unfold from the polar cap. Each thread is from 1/3 to 1/2 the length of the egg depending on the species, and ends in a small sticky knob. When fully expanded, this attachment structure

resembles a dandelion seed cap (Fig. 113). In this respect, Type I eggs are similar to those of *Ephemerella* (Koss, 1968).

Type II: (Figs. 116-120) Ovate, with 2 polar caps covered by a thick membrane; each cap contains long coiled threads (Fig. 119) resting on but not encircling egg (Figs. 116, 117); chorion smooth to finely punctate, with single micropyle (Fig. 118) and no sperm guide. The description of a sperm guide by Koss (1968) was shown to be in error by Koss (1969).

The Type II eggs of *C. latipennis* and *C. amica* were observed in water. Shortly after submersion, the thick cap membrane begins to dissolve and the entire cap separates from the egg, remaining attached by the thread ends (Fig. 118). A number of short, fine threads of uniform length and ending in small knobs unfold (similar to type I but fewer in number). Next, the main portion of the cap, which consists of a tightly bound cord of many long threads, begins to unwind; each of the individual threads is doubled back on itself so that the end of the cord consists of multiple loops (Fig. 120). Next, the individual threads gradually unravel, eventually resulting in a tangled mass of fine threads varying in length from 1/3 to 8 times the length of the egg and ending in variously sized knobs.

The time required for full deployment of the attached threads for both types of polar caps varies from a few minutes to over 1-1/2 hours. This great disparity may have some selective value in that it insures that eggs from a given female will be well dispersed, becoming attached to substrate at various times and places.

Fecundity varies greatly not only from species to species, but intraspecifically as well. For example, reported egg production for *C. amica* ranges from 95-1787 (Sweeney and Vannote, 1978, Rodgers, 1983). I found the following range in numbers of eggs from three individuals each of the following species: *C. anceps*, 448-567; *C. hilaris*, 414-806; *C. latipennis*, 812-2163.

The broad range of fecundity may be accounted for, in part, by the fact that there is some correlation between body size and the number of eggs produced (Clifford and Boerger, 1974). Reduced body size and fecundity may result when water temperatures are warmer or cooler than optimal thermal conditions during larval growth (Sweeney and Vannote, 1978). The smaller size of late emergers (especially in the case of multivoltine species) is generally related to faster development induced by higher water temperature regimes. Many character states, such as overall size and body pigmentation never reach their full potential in faster developing individuals (McCafferty and Pereira, 1984). Egg production in *Caenis* is also similarly affected. Not only is total fecundity reduced, but the eggs tend to be slightly smaller, and the size of the polar caps is often reduced.

The majority of caenis eggs, regardless of the type, range from 120-140 μ in length (excluding polar caps). The only exceptions are *C. anceps* and *C. macafferti* n. sp. which range from 140-170 μ .

The North American Caenis are placed in two species groups on the basis of numerous characters from larvae, adults and eggs. The diminuta group contains C. amica, C. candida, C. diminuta, C. latipennis, C. punctata, and C. youngi. The hilaris group contains C. anceps, C. hilaris, C. macafferti, n. sp., and C. tardata. Both groups show close affinities with species clusters in Western Europe. The diminuta group shares characters in common with the horaria-lineage and the hilaris group is comparable to the macrura-lineage as established by Malzacher (1984). Caenis bajaensis does not fall in either group and evidently may have been derived independently.

KEY TO THE NORTH AMERICAN SPECIES OF CAENIS

The larval key is based on mature specimens and may not be totally reliable for younger individuals. The larva of *C. candida* is not known. The adult key will reliably distinguish both males and females to the specific level.

Larvae

- Posterior margin of sternum 9 rounded or truncate (Figs. 40, 41); dorsal (outside) surface of forefemur with scattered setae only (Fig. 9); abdominal terga 9 and 10 usually with triads of black dots; abdominal sterna frequently with paired submedian black dots
- Posterior margin of sternum 9 notched (occasionally approaching truncate) (Figs. 42-45); dorsal surface of fore-femur with transverse row of spatulate setae in apical 1/3 (Figs. 15, 18-20, 82, 83); abdominal terga 9 and 10 and sterna never with black dots as above
- Middle portion of caudal filaments with whorls of short setae on every 2nd or 3rd segment, setae much shorter than space between whorls (Fig. 39)
- Middle portion of caudal filaments with long lateral setae on every segment, setae much longer than space between them (Fig. 38)
- Posterior margin of sternum 9 moderately notched (Fig. 42); operculate gills graded from pale basally to brown apically (Fig. 4); ventral surface of hind tibia with 0-2 fimbriate spurs in addition to marginal row of simple spurs; hind tarsal claw with 4-6 minute denticles (Fig. 27)

 C. anceps
- 3'. Posterior margin of sternum 9 deeply notched (Fig. 45); operculate gills uniformly brown (Fig. 7); hind tarsus with ventral row of 7-9 fimbriate spurs in addition to marginal row of simple spurs (Figs. 21, 84); hind tarsal claw with 20-25 minute denticles (Fig. 31).

 C. bajaensis
- 4. Abdominal terga 7-9 uniform brown (Fig. 6); posteromedian projection of abdominal tergum 2 (in dorsal view) narrowly triangular, at least twice as long as wide (Fig. 36)

 C. macafferti* n. sp.
- 4'. Abdominal terga 7-9 pale medially, brown longitudinal stripes or blotches laterally (Fig. 5); posteromedian projection of abdominal tergum 2 broadly triangular, approximately as wide as long (Fig. 35).

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- 5. Operculate gills with distinct brown and white pattern (Figs. 5, 50, 51); Y-ridge forked at or slightly basad of midlength of operculate gill, medial branch with 5-6 setae (Fig. 49); hind tarsus with 6-9 spurs along inner margin (Fig. 17); black lateral dashes usually visible on abdominal segments 7-9 (Fig. 5)

 C. hilaris

- 5'. Operculate gills uniform brown; Y-ridge forked distad of midlength of operculate gill, medial branch with 10-12 setae (Fig. 53); hind tarsus with 11-13 spurs along inner margin; no black lateral dashes on abdominal segments 7-9

 C. tardata
- 6. Posteromedian projection of abdominal tergum 2 long, straight, projecting upward, apex rounded in lateral view, truncate in dorsal view (Fig. 33); lateral margins of pronotum strongly divergent anteriorly (Fig. 8)

 C. youngi
- 6'. Posteromedian projection of abdominal tergum 2 of moderate length, hook-shaped in lateral view, triangular in dorsal view (Fig. 32); lateral margins of pronotum subparallel or but slightly expanded anteriorly (Figs. 2, 3)
- 7. Posterior margin of sternum 9 truncate (Fig. 41); hind femora with inner marginal setae almost as long as outer marginal setae (Fig. 12); hind tarsus with 5-7 fimbriate spurs on ventral surface (Figs. 13, 14); thorax usually with mottled color pattern (Fig. 3).

 C. latipennis
- 7'. Posterior margin of sternum 9 rounded (Fig. 40); hind femora with inner marginal setae much shorter than outer marginal setae (Fig. 10); hind tarsus with 6-11 (usually 9-11) fimbriate spurs on ventral surface (Figs. 11, 14); thorax usually uniform in color (Fig. 2).
- 8. Hind tarsal claw with 9-11 denticles of uniform size or becoming progressively larger toward tip (Fig. 22) *C. amica*
- 8'. Hind tarsal claw with 16-20 denticles, basal 4-6 larger than proceeding apical denticles (Figs. 23, 25) 9
- Antennal scape and pedicel usually stained with dark brown; hind tarsus with 9-11 fimbriate spurs on ventral surface
 C. diminuta
- 9'. Antennal scape and pedicel pale; hind tarsus with 6-8 fimbriate spurs on ventral surface *C. punctata*

Adults

- Black dots or dashes present on pleurities of at least some abdominal segments (Figs. 69, 72, 73-75, 77, 78)
- 1'. No black dots or dashes on abdominal pleurites (Figs. 71, 76, 79-81)
- 2. Vertex of head completely shaded with dark gray (Figs. 71, 79, 80) 3
- Vertex of head totally pale or at least pale on anterior or posterior 1/3 (Figs. 76, 77, 81)

- 3. Mid and hind femora and abdominal terga totally pale, unmarked (Fig. 71); wing vein ICuA1 forked with CuA1 basad of ICuA1-CuP crossvein (similar to Fig. 58); fleshy finger-like projection on abdominal tergum 2 (similar to Fig. 62); male forceps long, rounded, tip heavily sclerotized, with few or no microspines (as in Fig. 100); eggs with 2 type II polar caps (as in Fig. 109)

 C. candida
- Abdominal terga heavily shaded with dark gray or with lateral brownish purple blotches (Figs. 78, 80); mid and hind femora with or without black preapical dash; wing vein ICuA1 forked with CuA2 distad of CuA1-CuP crossvein (similar to Figs. 59, 60); no finger-like projection on abdominal tergum 2; male forceps short, flattened, densely covered with microspines (Figs. 105-111); eggs with type I or type II polar caps
- 4. Abdominal terga pale with brownish purple longitudinal stripes or blotches laterally (most pronounced on segments 1-3) (Fig. 79); outer margin of male forceps slightly undulating, apex with several long microspines (Fig. 109); eggs with type I polar cap (as in Fig. 114).

 C. tardata
- 4'. Abdominal terga heavily shaded with dark gray (Fig. 80); outer margin of male forceps straight, apex somewhat chisel shaped (Fig. 99, 111); eggs with type II polar caps (Fig. 116)

 C. bajaensis
- 5. Abdomen totally pale; thorax reddish brown; vertex of head with narrow transverse blackish brown stripe between lateral ocelli (Fig. 76) *C. anceps*
- 5'. Abdominal terga 1 and 2 with blackish purple shading, (Figs. 77, 81) occasionally with lateral blotches on 1-6; thorax light creamy-yellow 6
- 6. Abdominal tergum 2 with thin fleshy finger-like posteromedian projection (similar to Fig. 61); wing vein ICuA1 forking with CuA2 some distance distad of CuA1-CuP crossvein (similar to Fig. 60); median notal suture narrowly bordered with brown (Fig. 81)
 Amercaenis ridens
- 6'. Abdominal tergum 2 lacking finger-like posteromedian projection; wing vein ICuA1 forking with CuA2 proximal to CuA1-CuP crossvein (Fig. 59); mesothorax uniform light creamy yellow

 C. hilaris
- 7. Thorax light creamy-yellow; black dots or dashes present on abdominal pleura 2, 7-9 only; abdominal terga 1 and 2 with blackish purple shading, remaining terga usually pale (Fig. 77), occasionally with purplish black lateral blotches *C. hilaris*
- 7'. Thorax yellow-ocher to dark chestnut brown; black dots or dashes present on all abdominal pleura (often obscure on 3); abdominal terga 1-7 or 1-10 shaded with dark gray 8
- 8. Wing vein ICuA1 forked with CuA2 just distad of CuA1-CuP crossvein (similar to Fig. 59); abdominal terga 9 and 10 lacking triads of black dots; terga 1-10 heavily

shaded with blackish brown (Fig. 78); tergum 2 with fleshy finger-like posteromedian projection (Fig. 62); sterna light brown; eggs with single Type I polar cap (Fig. 115) (eastern U.S.)

**C. macafferti* n. sp.

- 8'. Wing vein ICuA1 forked with CuA1 basad of ICuA1-CuP crossvein (similar to Fig. 58); abdominal terga 9 and 10 with triads of black dots (lateral dots may be obscured by body pigmentation, median dot often elongated into a short dash) (Figs. 69, 72-75); tergum 2 with or without posteromedian projection; sterna pale, often with paired submedian black dots (similar to Fig. 70); eggs with 2 type II polar caps (as in Fig. 117)
- 9. Vertex of head completely shaded with dark gray (Figs. 69, 72, 74, 75) venter with irregular transverse black stripe between compound eyes (similar to Figs. 54, 55); abdominal terga 1-2 or 1-3 with black median line

 10
- 9'. Vertex of head pale in at least posterior 1/3 (Fig. 73), venter with 1 or 2 pair of submedian black dots (Fig. 56); anterior terga lacking black median line

C. latipennis

10. Hind femur with black preapical triangular spot or dash only (similar to Fig. 63)

11

- 10'. Hind femur with preapical black "V" shaped marking, usually engulfed in brownish black band more or less encircling femur (Figs. 64, 66)12
- 11. Abdominal tergum 2 with large fleshy finger-like projection (Fig. 61) C. youngi
- 11'. Abdominal tergum 2 lacking large finger-like projection *C. amica*
- 12. Hind femur and tibia usually with black speckles (Fig. 66); antennal scape and pedicel pale; male forceps very short and stocky, densely covered with microspines (Figs. 96, 103)

 C. punctata
- 12'. Hind femur lacking black speckles (Fig. 64); antennal scape and pedicel ringed with black (Fig. 55); male forceps of moderate length, with few microspines (Fig. 101)
 C. diminuta

Diminuta Group

LARVA: Forefemur with scattered setae only (Fig. 9); mid and hind tarsi with ventral row of 5-11 fimbriate spurs (Figs. 11, 13, 14); posterior margin of abdominal sternum 9 truncate to rounded (Figs. 40, 41). Fully pigmented individuals with triads of black dots on abdominal terga 9 and 10 (Figs. 2, 3), and paired submedian black dots on most abdominal sterna.

In general, the body tends to be broader with lateral abdominal projections more pronounced, and the tarsal claw denticles larger and more numerous in the *diminuta* group compared to the *hilaris* group.

ADULTS: Wing vein ICuA1 forked with CuA1 basad of ICuA1-CuP crossvein (Fig. 58); marginal setae not extending beyond medial sector. Tips of male forceps heavily sclerotized, with few or no microspines (except *C. punctata*) (Figs. 100-104); fully pigmented individuals

(except *C. candida* on which there are no abdominal markings) with black dots on abdominal pleura 2 and 4-9; abdominal terga heavily pigmented; terga 9 and 10 with triads of black dots (Figs. 69, 72-75); paired submedian black dots usually present on most abdominal sterna (Fig. 70). In general, adults in this group are larger than those in the *hilaris* group, males ranging from 2.5-4.5 mm.

EGGS: With two Type II polar caps (Fig. 117)

BIOLOGY AND ECOLOGY: The larvae of most species in the *diminuta* group occur on a broad range of substrate types but are most commonly encountered in silt-laden, still water habitats of lakes, ponds, and backwater areas of rivers and streams. Larvae have been reported in association with various aquatic plants (Berner, 1950, Edmunds, et al. 1976). My observations indicate that the association is with the depositional area created by emergent vegetation and not with the plants themselves.

The time and length of the emergence period varies greatly from place to place. It appears to be influenced not only by latitude, but also by local climatic and aquatic thermal conditions. These conditions also appear to affect the number of generations per year. Data presented by Clifford (1982) indicate that the life cycle of many populations is quite flexible and may involve both univoltine (mainly univoltine summer) and multivoltine (mainly bivoltine winter-summer) cycles.

Caenis amica Hagen

Caenis amica Hagen, 1861: 55. Type locality: Baltimore [MD?]. Type deposition: (M) MNB. Caenis diminuta (in part), Eaton, 1884: 147.

Caenis amica, McDunnough, 1931: 256.

Caenis simulans McDunnough, 1931: 263. Type locality: Orillia, Ontario. Type deposition: (M) CNC. NEW SYNONYMY.

LARVA (Fig. 2): Body length 4.5-6.5 mm.

Head.— Vertex predominantly medium brown, somewhat lighter surrounding lateral ocelli, darker brown at posterolateral margins. Antennae pale.

Thorax.— Pronotum medium brown, variously marked with dark brown; large submedian pale blotches usually present; pair of small black submedian dots near posterior margin; lateral margins pale, subparallel or slightly expanded anteriorly. Mesonotum usually uniform medium brown, rarely mottled; large pale spots at wing bases; short black dashes with superimposed white spots mesad of wing bases. Sterna pale. Legs pale; black dots and short dashes on coxae; small black anteroapical spot on trochanters; femora with black subapical dash, usually joining light brown band on mid and hind femora; light brown bands at base of tibiae and middle of tarsi; dorsal (outside) surface of forefemur with scattered simple setae only (Fig. 9); inner marginal setae of mid and hind femora much shorter than outer marginal setae (Fig. 10); hind tarsus (Fig. 11, 14) with 12-14 spurs along inner margin and row of 9-11 fimbriate spurs ventrally; hind tarsal claw (Fig. 22) with 9-11 denticles of uniform length or becoming progressively larger toward tip.

Abdomen.— terga 1 and 2 medium brown mesially, dark blackish brown sublaterally, pale laterally, narrow blackish stripe along median line often visible; terga 7-9 pale medially, brown laterally, dark blackish brown at anterolateral margins (most pronounced on segment 7); tergum 10 uniform medium brown; terga 9 and 10 each with triad of black dots. Posteromedian projection of tergum 2 acute, of moderate length (Fig. 32); posterolateral projections of middle segments will developed, segment 5 approximately 5 times as wide as long (Fig. 40). Venter pale; posterior sterna usually with 2 pair of obliquely arranged

submedian black dots; posterior margin of sternum 9 rounded (Fig. 40). Operculate gills uniform blackish brown except for small pale area at base; dorsal surface with sparse, minute spicules (Fig. 88); medial and apical branches of Y-ridge with long setae (Fig. 48). Caudal filaments with alternating pale and light brown banded segments; each segment in middle portion of filaments with long lateral setae, setae much longer than space between them (Fig. 38).

ADULT MALE (Fig. 69): Body length: 2.8-4.5 mm.

Head.— Vertex entirely suffused with dark gray. Venter pale with irregular transverse black band between compound eyes (Fig. 54). Antennae pale.

Thorax.—Pronotum pale yellow; median and anterolateral areas suffused with dark gray; lateral and posterior margins edged with black; black submedian dashes near posterior margins, often joining black posterior margin. Mesonotum medium to dark bronzy brown; prescutum black; oblique black dashes at wing bases; indistinct blackish dashes or dots along base of posterior parapsidal sutures; scutellum light smoky. Pleura only slightly lighter than notum; primary sutures black. Sterna pale; small black submedian dots on metasternum between hind coxae. Legs pale; coxae with blackish streaks on outer surface; forefemur stained with dark gray; narrow black preapical streak on dorsal edge; mid and hind femora with preapical black triangular dash (Fig. 63). Wings with marginal setae not extending beyond medial sector (Fig. 59).

Abdomen.— Terga 1 and 2 (sometimes 3) pale laterally, dark gray sublaterally, median 2/3 pale except for narrow black median line; terga 3-6 or 4-6 with dark gray shading in median 2/3 and pale lateral borders; terga 7 and 8 with anterolateral triangular dark gray blotches; terga 9 and 10 each with triad of black dots. Pleura 2 and 4-7 (rarely 3) with black dots or dashes, most pronounced on pleurum 7. Venter (Fig. 70) pale, black submedian dots usually present on all sterna (normally two pair of obliquely arranged dots on posterior segments); occasionally with black median blotch on each sterna; black dots at junction of sterna and pleura on segments 1-7. Genital forceps (Fig. 94, 100) faintly smoky, of moderate length, rounded, slightly curved, and with few microspines. Caudal filaments pale.

ADULT FEMALE: Body length 4.0-6.0 mm.

TAXONOMY: Eaton (1884) synonymized *C. amica* with *C. diminuta*. McDunnough (1931) reinstated *C. amica* as a valid species. He did not examine the type material, and his decision was based on a detailed description provided to him by G. Ulmer.

Two male specimens that had been designated as syntypes of *C. amica*, are located in the MNB. Hagen (1861) had included both specimens as types. His original description was, however, based on but one of these specimens and he noted that the second specimen differed significantly from the first and possibly represented a different species. I have examined both of Hagen's specimens and, as he suspected, they do represent two different species. The one that fits his original description is here designated as the lectotype and is so labeled on the MNB collection. The second specimen represents a misidentified specimen of *C. anceps*. The local label on the lectotype simply reads "Baltimore." It is presumed to be Baltimore, Maryland; however, Hagen gave the distribution as "Pennsylvania."

Traver (1935) redescribed *C. amica* based on specimens from multiple collection sites along the east coast. Since that time her concept of the species has been followed. Unfortunately, the specimens which were assumed by Traver to be *C. amica* were misidentified and are actually *C. maccafferti* n. sp.

McDunnough (1931) also described *C. simulans*, one of the most commonly encountered specific *Caenis* names in the literature. Based on my examination of the types of this species,

the types of *C. amica*, and large numbers of specimens from throughout the continent, *C. simulans* is placed as a junior synonym of *C. amica*.

Smith (1935) described the eggs of C. amica (as C. simulans). He also described what he thought were the eggs of C. amica according to Traver's concept of the species (= C. macafferti n. sp.); however, this latter species was apparently misidentified. It fits representatives of the diminuta group and not C. macafferti n. sp., which is in the hilaris group.

Koss (1968, 1969) observed three different forms of the supposed eggs of *C. amica* (under the name *C. simulans*), raising speculation that there may be more than one species involved. I have observed considerable interspecific variation in both the shape and size of the polar caps of *C. amica*. This variation exists not only between populations and individuals within a population, but between eggs of a single individual. The differences observed by Koss fall within the range of my own observations and I am convinced that they are the result of normal variability.

A color drawing was included on the frontis plate of "the Biology of Mayflies" (as *C. simulans*) (Needham, Traver, and Hsu, 1935). However, it is not sufficiently detailed to be diagnostically valuable. Burks (1953) included a whole dorsal drawing of the larva.

The larvae of *C. amica* are difficult to separate from those of *C. punctata* and *C. diminuta*. All three species are similar in general coloration and morphology. The configuration of the hind claw denticles is the most reliable character I have found. *Caenis* amica has 9-11 denticles which are of uniform length or, more often, become gradually larger toward the tip. *Caenis punctata* and *C. diminuta*, on the other hand, have 16-20 denticles, the basal 4-6 being much larger than the proceeding ones. The dark preapical banding on the femora of *C. punctata* and *C. diminuta* and the darkened scape and pedicel of the latter species may also be helpful but must be used with caution. *Caenis latipennis*, which frequently occurs in association with *C. amica*, has a truncate 9th sternum as opposed to being rounded on *C. amica*, 5-7 ventral fimbriate spurs on the hind tarsus as opposed to 9-11 on *C. amica*, and the inner and outer marginal femoral setae are subequal in length. The vast majority of *C. latipennis* larvae have an overall mottled color pattern, whereas the vast majority of *C. amica* are of uniform color. This last character, however, is not totally reliable.

Adults of C. amica are most easily confused with C. punctata and C. diminuta. The dark preapical bands on the mid and hind femora of heavily pigmented specimens of these two species easily distinguish them from C. amica. This banding may be totally absent on lighter individuals; however, the black preapical V-shaped mark remains distinctive in C. punctata and C. diminuta. The equivalent mark on C. amica is either a simple dash or, at most, an elongate triangle. The male forceps of C. amica are moderately long, thin, and slightly bowed, whereas those of C. punctata are very short and stocky. Caenis punctata usually has paired submedian black dots near the anterior margin of the vertex and just ventrad of the frontal ridge of the head, and black speckles on the mid and hind femora. These markings are usually absent in C. amica. I have, however, seen a few individuals of C. punctata that lack femoral speckles and a few C. amica on which these speckles were present. The antennal scape and pedicel of C. amica is totally pale. The antennal scape and pedicel of C. diminuta are ringed with black. McDunnough (1931) and Traver (1934) described the male forceps of C. diminuta as short (similar to C. punctata). Although the forceps are somewhat variable, the vast majority are closer in length and shape to the forceps of C. amica. This genital character can not effectively be used to separate these two species.

BIOLOGY AND ECOLOGY: This is the most widespread and one of the most commonly encountered *Caenis* in North America. Under appropriate conditions it occurs in extremely

large numbers. It has been reported from all southern Canadian Provinces and from all but a few States (Map 1). It was not reported from Florida or the Carolinas by Berner (1977); however, my examination of collections from these states revealed a number of *C. amica* mixed in with lots labeled as *C. diminuta*.

Adults emerge throughout the warmer months. Berner (1977) reported adult collections from March through November from the Southeast. Emergence time is more restricted at northern latitudes. Adult emergence takes place from dusk until about one hour after dark. Edmunds et al. (1976) indicated that *C. amica* has two successive generations per summer. The work of Rodgers (1982, 1983) involving biothermal channels in Alabama supported this possibility. Sweeney (1976) and my own observations indicate that, in Pennsylvania and Indiana, it may be univoltine with multiple broods.

Larvae may be encountered in almost any freshwater habitat, but they prefer areas with little or no current such as lakes, ponds, and the slower reaches of rivers and streams. Although they occur on a wide range of substrates such as fine sand, mixed gravel and submerged debris, they are most commonly encountered in organically rich silty areas.

MATERIAL: Lectotype, M, *Caenis amica*, Baltimore [MD?], Zimmerman (M). Holotype, M, *Caenis simulans* ONTARIO; Orillia, VII-21-?, C.H. Curran (CNC); Allotype, F, same as Holotype (CNC); Paratypes, 9 M, 11 F, same as Holotype (CNC).

Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 9806 adults, 693 larvae). ALBERTA: Parkland, Clifford E. Lee Nature Sanc., VIII-16-1979, Corkum, 200 MF, (PERC); Waterton Lakes, VII-6-9, 4 M (CNC). ALABAMA: Henry Co., Chattahoochee Riv. 8 mi S of George Lock Dam, X-3-1971, Carlson 4 F (FAM); Morgan Co., TVA Brown Ferry Biothermal Channels, IV-14-1980, Rodgers, 4 M, 5 F (L. Rodgers). ARIZONA: Yavapai Co., 18 mi N of Jerome, VI-5-1955, Selander, 4 F (UU). ARKANSAS: Boone Co., Bear Cr. at St Rd 14, 3 mi W of jct Hwys 281-14, V-28-1974, McCafferty, et al., 25 MF (PERC); Pike Co., Lake Greeson, III-29-1981, Bacon, 10 L (PERC); BRITISH COLUMBIA: Shuswap Lk., VII-30-1952, Leech, 100 M (CAS). CALIFORNIA: Lassen Co., Eagle Lk. Field Station, Mohogany Lk., VII-8-1970, Smith, 500 MF (FAM); Sierra Co., Webber Lk., VIII-2-1958, 8 M (CAS); Siskiyou Co., Castle Lk., VII-21-1953, Chandler, 38 M (CAS). CONNECTICUT: Middlesex Co., Killingworth, VIII-1982, Main, 2 M, 25 F (PMNH); New Haven Co., Mt. Carmel, V-20-IX-6-1960, 8 M, 45 F (PMNH). FLORIDA: Liberty Co., Creek 1 mi W of Ochlockonee Riv. at Hwy 20, IV-3-1974, Carlson, 6 M (FAM); Marion Co., Oklawaha Riv., IV-10-1948, Berner, 11 M (UU); Okaloosa Co., Blackwater Riv., Florida A & M Univ. Biol. Station, 4.5 mi NW of Holt, V-11,12-1971, Tsue and Pescador, 50 MF (FAM); Orange Co., Winter Park, III-12-1978, Beck, 21 M, 3 F (VPI). GEORGIA: Baker Co., Flint Riv. at Newton, IX-11-1971, Carlson, 3 M, 2 F (FAM); Bartow Co., Clear Lake at Cassville, IV-20-1946, Fattig, 50 MF (INHS). IDAHO: Bonner Co., Sandpoint, VIII-9-1951, Morton, 2 M, 1 F (UU); Twin Falls Co., 4 mi W of Milner, IX-3-1944, Edmunds, 77 MF (UU); Blaine Co., Pettit Lake, VII-12-1959, Leech, 35 M (UU). ILLINOIS: Fulton Co., Illinois Riv., Banner, VIII-8-1939, Hansen, 24 M (INHS); Lake Co., Palos Park, Mud Lake, VIII-4-1937, Ross and Burks, 75 MF (INHS); Randolph Co., Mississippi Riv., Chester, V-11-1932, Ross and Mohr, 200 MF (INHS); INDIANA: Delaware Co., West Fork White Riv., Tillotson, VIII-4-1977, 50 MF (PERC); Elkhart Co., Elkhart Riv. at Elkhart Riv. Preserve nr Benton, VIII-2-1977, Minno and Yocum, 4 F, 1 L (PERC); Fulton Co., Mud Cr. at Hwy 14, 5 mi W of Rochester, McCafferty, et al., 75 MF

(PERC); Miami Co., Pond at Miami-Wabash Co. line, Hwy 124, V-14-1974, Provonsha, 100 MF, (4 M, 2 F reared with LCS), 14 L (PERC); Morgan Co., Martinsville, VII-8-1983, Provonsha, 5 M, 2 F (1 M, 1 F reared with LCS), 25 L (PERC); Parke Co., Small pond, V-20-1972, Delp, 150 MF (PERC); Spencer Co., Lake Lincoln, Lincoln St. Pk., V-7-1972, McCafferty, et al., 1500 MF, 12 L (PERC); Steuben Co., Fawn Riv. at Orland, V-29-1975, Provonsha, 100 MF, 2 L (PERC); Tippecanoe Co., Entm. Res. Area Pond, V-IX-1982, Provonsha, 800 MF, 80 L (PERC). IOWA: Dickenson Co., West Lake Okaboji, VII-25-1967, Reimer, 1 M (ANSP); Okoboji Co., Lake Okoboji, VIII-10-1942, Adams, 65 L (CNC); Osceola Co., Ocheyedan, VII-26-1975, Lago, 2 F (UM). KANSAS: Atchison Co., SW end of Atchison Co., St. Lk. and Pk., V-22-1978, Slater, 8 F (PERC); Crawford Co., Lake Crawford, VIII-4-1976, Oldham, 3 L (UK); Mitchell Co., Solomon Riv. below dam at Beloit, VIII-4-1977, Roth, 3 F (UK). KENTUCKY: Bath Co., Trib of Salt Lick Cr. at Clear Cr. Furnace Campground, VI-4-1973, McCafferty, et al., 1 M, 1 F (PERC); Bullitt Co., Crooked Cr. at L & N Railroad Crossing, VIII-3-1983, 6 L (PERC); Christian Co., Buck Fk. Pond Riv., at KY 107, VIII-14-1980, 2 L (PERC); Harlan Co., Harlan, VI-12-1940, Frison, et al., 1 M (INHS); Muhlenburg Co., Green Riv. nr Central City, IX-1-1961, Roback, 4 L (ANSP). LOUISIANA: Caleasieu Co., Calcasieu Pk., III-10-1939, Hubbell, 5 M (UF); Lafayette Co., Lafayette, III-15-1952, Sublette, 1 M (UF). MAINE: Hancock Co., Elsworth, VI-18-1976, McCafferty, et al., 3 F (PERC); Kennebec Co., Gard, VI-21-1975, Dill, 3 M, 2 F (PERC); Knox Co., Union, VIII-18-1939, Frison, 9 M, 15 F (INHS). MANITOBA: Aweme, VI-14-?, 12 MF (CNC). MASSACHUSETTS: Hampshire Co., Amherst, V-28-1955, Flint, 2 M, 3 F (UU); MICHIGAN: Allegan Co., Douglas Lk., VIII-10-1948, Edmunds, 50 M, 3 F (UU); Chebougan Co., VII-14-1932, Nottingham, 25 M, 2 F (CNC); Clinton Co., T5N, R1W1 Sec. 23, VI-8-1965, Donahue, 75 MF (PERC); Montcalm Co., T11N1R8W1, Sec 33, VII-8-1966, Donahue, 12 M (PERC); Traverse Co., Headquarters Lk., VI-13-1966, 50 MF (PERC). MINNESOTA: Ithasca Co., Itasca St. Pk., Lake Itasca, VII-15,20-1965, Maschwitz, 3 M, 3 L (UMSP); Jackson Co., Kilen Woods St. Pk., VII-16-22-1972, 1 M, 1 F (UMSP); Kittson Co., Lake Bronson St. Pk., VIII-13-19-1972, 2 F (UMSP); Lake Co., Moose Lake 20 mi E of Ely, VI-17-1981, Edwards, 50 MF (PERC). MISSISSIPPI: Bolivar Co., 2 mi S of Rosedale, XI-3-1980, Lago, 15 M, 5 F (UM); Lafayette Co., 8 mi NE of Oxford, X-1-1976, Barris, 3 M, 7 F (UM); Jasper Co., 6 mi NW of Montrose, V-7-1980, Lago, 25 MF (UM); Rankin Co., 10 mi NE of Canton, V-6-1980, Lago, 10 M, 15 F (UM); Winston Co., 13 mi W of Louisville, V-8-1980, Lago, 15 M, 1 F (UM). MONTANA: Fallen Co., Baker Lk., VI-26-1974, Roemhild, 2 L (MTSU); Flathead Co., Whitefish Lk., VII-15-1970, Edmunds, 90 MF (UU); Petroleum Co., King Ck., 1.5 mi S, 5 mi W of Winnett, VII-14-1971, Rees, 8 F (USNM); Phillips Co., Nelson Res., VI-8-1977, Roemhild, 5 M, 1 F (MTSU). NEBRASKA: Cass Co., Weeping Water Cr., pond behind dam, IV-13-1977, Maret, 11 L (UNL); Cherry Co., Sparks, VII-10-16-1977, 9 M, 35 F (UNL); Dawes Co., Niobrara Riv., below Box Butte Res. Dam, VI-15-1984, McCafferty and Provonsha, 5 M, 10 F, 6 L (PERC); Douglas Co., Papio Cr. behind damsite 16, IV-7-1979, Pruess, 5 L (UNL); Holt Co., VI-1974, Pruess, 50 MF (UNL); Pawnee Co., Johnson Cr., IV-15-1980, Pruess, 24 L (UNL); NEW HAMPSHIRE: Cheshire Co., Connecticut Riv. at Brattlesboro, VI-19-1976, McCafferty, et al., 1 M (PERC). NEW JERSEY: Cape May Co., Dennis Creek, Lk., V-1-1976, Dotterweich, 7 L (VPI); Mercer Co., Carnegie Lk. at Princeton, VII-11-1967, Richardson, 12 L (ANSP). NEW YORK: Tompkins Co., Ithaca, Cornell Agron. Ponds, VIII-16-1965, Cooper, 25 MF (PERC); Franklin Co., Fish Cr. Ponds Campsite, VI-15-1976, McCafferty, et al., 9 M (PERC). NORTH CAROLINA: Orange Co., Eno Riv., V-5-1981, 19 L (SWRC). OHIO: Logan Co., Indian Lk., VI-17-1941, Frison and Ross, 3 F (INHS); Richland Co., Lucas, VIII-9-12-1965, 15 M, 1 F (UU). OKLAHOMA: Latimer Co., Turkey Cr., 6 mi E of Red Oak, VI-5-1973, Stark, 1 M (UU). ONTARIO: Algonquin Prov. Park, Mew Lake, VII-8-1966, Koss, 50 MF (PERC); Reed Narrows, Lake of the Woods, VIII-23-1938, Baldof, 2 M (INHS); The Marsh, Pt. Pelee, VI-4-1929, Walley, 28 L (CNC); Go Home Bay, VII-3-1932, Walley, 80 M, 6 F (CNC); Normondale, VI-4-1931, Walley, 4 M (CNC); Station Is., Georgia Bay, VII-4-1912, 12 M (CNC). OREGON: Klamath Co., Klamath Falls, IX-14-1938, Jewett, 18 M, 4 F (INHS). PENNSYLVANIA: Adams Co., Rock Cr. at Gettysburg Battlefield, VII-27-1956, Roback, 9 L (ANSP); Chester Co., E. Br. White Clay Cr., Stroud Estate, Rt 926, VII-24-1968, Richardson, 1 M (SWRC); Wyoming Co., Meshoppen Cr. 1.6 mi E of Meshoppen, VI-23-1980, 1 L (SWRC). QUEBEC: Baie James, Programme 55, VII-16-VIII-18-1975, 2 M (UMSP); Knowlton, VII-20, 4 M, 1 F (CNC). SASKATCHEWAN: Attons Lake, VII-11-1946, Brooks, 6 M (CNC); Indian Head, VII-10,11-?, 6 M (CNC); Pond 8 mi E of Saskatoon on Hwy 5, VI-26-1973, Smith, 3 M, 2 F (US). SOUTH CAROLINA: Aiken Co., Savannah Riv. Plant, Upper Three Runs Cr., III-29-1977, Herlong and Prichard, 1 M, 2 F (CUC); Newberry Co., Indian Cr., 5 mi SSE of Whitmire, V-20-1981, 3 L (SWRC). SOUTH DAKOTA: Pennington Co., Rapid City, VI-13-1975, McCafferty, et al., 13 M, 1 F (PERC). TENNESSEE: Fentress Co., Burville, V-5-1960, Benesch, 1 M (UF); Obion Co., Reelfoot Lk., Bio Station, V-22-1954, Edwards, 5 M (UU); Putnam Co., Lake nr I-40, Dry Valley Area, V-14-1976, Kondratieff, 8 M, 2 F (reared with LCS) (FAM). TEXAS: Austin Co., San Bernard Riv. at I-10 nr Sealy, V-9-1977, McCafferty et al., 9 M, 4 F, 25 L (PERC); Jasper Co., Neches Riv. at US Hwy 69, V-4-1977, McCafferty, et al., 10 M, 1 F (PERC); Orange Co., Sabine Riv. at Cow Bayou, VIII-1-1969, Richardson and Fuller, 2 L (ANSP). UTAH: Daggett Co., Flaming Gorge, Greens Lk., VI-27,28-1973, 20 M, 5 F (USNM); Salt Lake Co., Haynes Lk, VII-1-1954, Edmunds, 600 MF (UU); Uintah Co., Pelican Lk., V-31-1976, Edmunds, 45 M., 30 MF (2 M reared with LCS) (UU); VIRGINIA: Accomack Co., Assateque, IX-10-1972, Cross, 16 M (USNM); Hanover Co., North Anna Riv. Falls, VI-2-1977, Kondratieff, 3 M (VPI); Montgomery Co., Pond nr Tom's Cr. at Rt 655, IV-19-1977, Powell, 2 F (reared with LCS) (VPI); Nottoway Co., Little Nottoway Riv. 2 mi S of Crewe, VI-16-1980, Kirchner, 28 M, 3 F (VPI); Rockingham Co., College Pond, IV-10,20-1976, Bodkin, 5 L (VPI); Scott Co., Gilleys Pond, V-4-1974, Simont, 3 L (VPI); Virginia Beach Co., Back Bay, VIII-30-1975, Knausenberger, 1 F (reared with LCS) (VPI). WASHINGTON: Stevens Co., Loon Lake VI-1953, 7 F (UU). WEST VIRGINIA: Pendleton Co., Gandy Cr., Spruce Knob, VI-22-1973, 1 M (USNM). WISCONSIN: Iron Co., Lake of the Falls, VI-23,24-1984, Bloodgood, 35 M, 15 F (PERC); Vilas Co., Trout Lk., VII-4-1939, Nelson, 16 M, 8 F (INHS); Walworth Co., Bigfoot Beach St. Pk., VI-20-1957, 17 M (PERC); WYO-MING: Carbon Co., Platte Riv. nr Sinclair, VI-6-1961, Edmunds, 1 L (UU).

Caenis candida Harper and Harper

Caenis candida Harper and Harper, 1981: 1787. Type locality: Lac Low, Quebec, Canada. Type deposition: (M) CEUM.

LARVA: Unknown.

ADULT MALE (Fig. 71): Body length: 4.0-4.5 mm.

Head.— Vertex mottled with dark gray, posterior margin finely lined with black; venter pale, unmarked. Antennae pale yellow.

Thorax.— Pronotum pale yellow, large posterolateral brownish black blotches; anterolateral margins edged with black. Mesonotum and pleura dark brown; prescutum and all major sutures black. Sterna pale yellow. Legs pale yellowish white; forecoxa margined with dark brown; forefemur suffused with tan, and with a dark longitudinal streak extending its full length on the outer surface; mid and hind legs without darker markings.

Abdomen.— Pale yellow, without darker markings; tergum 2 with thin posteromedian finger-like projection (similar to Fig. 61). Genital forceps rounded, of moderate length, slightly curved, with few or no microspines. Caudal filaments pale.

ADULT FEMALE: Body length 5.0 mm.

TAXONOMY: The totally unmarked yellowish mid and hind legs and abdomen distinguish it from all other members of the *diminuta* group. Within the *diminuta* group, the finger-like projection on abdominal tergum 2 is shared only with *C. youngi*. Based on the presence of this projection on the adult, it is predicted that the larva will also possess a rather large posteromedian projection, perhaps closely resembling that of *C. youngi*.

BIOLOGY AND ECOLOGY: This species is presently known only from Lac Low and Riviere du Caster in northwestern Quebec (Map 2). Adult records are from July 18-August 13. The larvae probably inhabit similar environments as other members of the *diminuta* group.

MATERIAL: Paratypes, 3 M, QUEBEC: Riv. Castor, P.L. Baie James, VII-18-1975, Harper and Harper (CEUM); Paratype, F, Lac Low, P.L. Baie James, VIII-13-1973, Harper and Harper (CEUM).

Caenis diminuta Walker

Caenis diminuta Walker, 1853: 584. Type locality: St. John's Bluff, E. Florida. Type Deposition: BMNH.

Caenis amica, Eaton, 1884-147.

LARVA: Body length 4.0-5.5 mm.

Head.— Vertex light to medium bronzy brown; area posterior to transverse epicranial suture covered with finely reticulated dark brown pattern. Antennal scape and pedicel usually shaded with blackish brown; flagellum light tan.

Thorax.— Pronotum light to medium bronzy brown with darker brown sublateral shading; paired submedian black dots near posterior margin; lateral margins pale, subparallel. Mesonotum usually uniform light to medium bronzy brown with diffuse darker brown shading, occasionally mottled with light yellow speckles, large black spots at wing bases. Legs yellowish white; each femora with a blackish brown subapical band; dorsal surface of forefemur with scattered setae only (similar to Fig. 9); inner marginal setae of mid and hind femora much shorter than outer marginal setae; hind tarsus with row of 12-14 spurs along inner margin and ventral row of 9-11 short fimbriate spurs (similar to Figs. 11,14); hind tarsal claw (Fig. 23) with 14-20 denticles (basal 4-6 denticles larger than proceeding apical ones).

Abdomen.— Tergum light yellow-brown; terga 1 and 2 with narrow median and broad sublateral blackish brown longitudinal stripes; tergum 7 with dark suffuse transverse band anteriorly; terga 7-10 with sublateral longitudinal brown blotches; terga 9 and 10 each with triad of black dots; posteromedian projection of tergum 2 triangular and of moderate length (similar to Fig. 32); lateral projections of middle segments well developed, segment 5 approximately 5.5-6.0 times as wide as long (similar to Fig. 40). Sterna pale; each sternum

with blackish brown botch near lateral projections forming abbreviated longitudinal stripes the length of the abdomen; obliquely arranged black dots usually visible on 6-9 or 7-9 and single sublateral dots on anterior sterna similar to adult pattern; posterior margin of sternum 9 rounded (similar to Fig. 40). Operculate gills dark blackish brown with sparse, minute spiculations on dorsal surface (as in Fig. 88); medial and apical branches of Y-ridge with long setae (similar to Fig. 48). Caudal filaments faintly banded on alternating segments, each segment in middle portion of filaments with long lateral setae, much longer than space between them (similar to Fig. 38).

ADULT MALE (Fig. 72): Body length 2.7-3.8 mm.

Head.— Vertex entirely shaded with dark gray; venter with irregular black transverse line between eyes. Antennae pale; scape and base of pedicel heavily shaded with black.

Thorax.— Pronotum pale, with suffused dark gray shading, darkest medially; lateral and posterior margins narrowly bordered with black; black submedian dots usually present near posterior margin. Mesonotum medium to deep bronzy-brown; prescutum dark brown; black transverse dashes at wing bases usually joining smoky longitudinal blotch along lateral margin of lateroscutellum; posterior lateroscutellum usually slightly darker brown than remainder of mesonotum; faint blackish V-shaped dash following base of posterior parapsidal sutures; scutellum pale smoky. Pleura medium bronzy brown, heavily shaded with black; primary sutures narrowly marked with black; anterior margin of metapleuron heavily black. Sterna pale; laterosternal sutures anterior to furcal pits black; metasternum with submedian black dots between hind coxae. Forecoxa, trochanter, and femur lightly tinged with smoky brown; femur with apical brown band. Mid and hind legs pale; coxae with 2 narrow black dashes; femora with black subapical dash on dorsal margin encompassed by brownish black band that usually encircles femora (Fig. 64).

Abdomen.— Terga 1-6 heavily shaded with dark gray; terga 1, 2 and base of 3 pale in median area with black mid-dorsal line; posterior margins of terga 1-6 black; terga 7-10 mostly pale; terga 7 and 8 with faint submedian gray blotches; 9 and 10 each with triad of black dots. Pleurum pale with distinct black dots on both dorsal and ventral surface of all pleura. Sterna pale; usually with pairs of obliquely arranged sublateral black dots on segments 6-9 or 7-9 and single sublateral dots on anterior segments (similar to Fig. 70). Genital forceps (Fig. 101) pale, rounded, relatively short and stocky, with few microspines. Caudal filaments pale.

ADULT FEMALE: Body length 3.2-4.5 mm.

TAXONOMY: Walker (1853) described *C. diminuta* from a single male. Although I have not seen this type, Spieth (1941) did examine it and concurred with McDunnough's (1931) and Traver's (1935) redescriptions of the species. (Traver's description was for the most part taken from McDunnough). Spieth did note a few characters not included in these previous descriptions. Adults I have assigned to *C. diminuta* agree with the descriptions of McDunnough, Traver, and Spieth. These workers, however, did not mention the darkened antennal scape and pedicel, a character I have found most helpful in separating *C. diminuta* from others in the group.

This is one of the few North American *Caenis* previously illustrated. Berner (1950) included whole dorsal drawings of both the adult male and the larva.

The larvae are very similar in appearance to larvae of both *C. amica* and *C. punctata*. They can be separated from *C. amica* by the number of denticles on the hind claws. *Caenis diminuta* has 4-5 large basal denticles followed by 12-15 smaller denticles, for a total of 16-20, whereas *C. amica* has only 9-11 denticles, which are of uniform length, or more typically

become progressively larger toward the tip of the claw. The only morphological character I have found to separate larvae of *C. diminuta* from *C. punctata* is the number of fimbriate spurs on the ventral surface of the hind tarsus; *C. diminuta* has 9-11, *C. punctata* has 6-8. The thoracic coloration of *C. diminuta* is usually somewhat darker than that of *C. punctata*, the darkened antennal scape and pedicel will usually separate it from *C. punctata* as well as *C. amica*. These color characters are somewhat variable and should be used with caution.

Adults can consistently be separated from others in the group by the darkened antennal scape and pedicel. The darkened femoral band on the mid and hind legs will also usually separate it from all species except *C. punctata*. On some individuals, however, this band is abbreviated and closely resembles the leg markings of *C. amica. Caenis* punctata usually possesses similar banding on the femora; however, it also usually possesses black speckling on the femora and occasionally on the tibiae as well. Speckling is never present on the femora of *C. diminuta*. In addition, the thorax of *C. diminuta* is usually much darker than *C. punctata*. Although earlier authors have reported the male forceps as "short," the length is about halfway between that of *C. amica* and *C. punctata*.

BIOLOGY AND ECOLOGY: The main range of *C. diminuta* (May 3) encompasses most of the south-eastern United States where it tends to be the most common *Caenis* species. It was previously thought to be the only member of the *diminuta* group that occurred in the far Southeast. My reexamination of previously identified collections revealed the presence of both *C. amica* and *C. punctata* from Florida and the Carolinas. McDunnough (1931) identified a series of specimens from Ontario, Canada as *C. diminuta*. I have examined these specimens and agree with his identification. I have also seen large series from Nova Scotia, Minnesota, Michigan, Wisconsin, and Maine. It is possible that the range of this species will eventually be found to encompass most of eastern North America.

Berner (1950) discussed the biology and life cycle of C. diminuta in detail. He reared adults from eggs in four months. The time required for hatching the eggs varied from five to eleven days. Berner (1977) records adult emergences in the South from March through November.

Like other members of the group, the larvae are found predominently in lakes, ponds, or still water areas of rivers and streams with rich deposits of silt and detritus. They are often found in association with emergent vegetation.

MATERIAL: Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 3784 adults, 157 larvae). ALABAMA: Perry Co., Cahoba Riv., St. Hwy 183, VI-27,28-1968, Peters, et al., 1 M (FAM). FLORIDA: Alachua Co., Lake Alice, X-28-1938, Berner, 2 M, 1 L (UU); Dade Co., South Miami Canal, VI-11-1978, 10 L (UU); Jefferson Co., Monticello, V-1968, Whitcomb, 100 MF (FAM); Gadsden Co., Rocky Comfort Cr., 7 mi S of Quincy, IV-16-1967, Peters, 20 M, 35 F (FAM); Hernadndo Co., Weekanatchee Riv., II-20-1954, Berner, 500 F (UF); Highlands Co., Archbold Bio. Sta., III-19-1979, Beck, 75 MF (VPI); Levy Co., Otter Cr., IX-19-1959, Berner, 1000 MF (UF); Marion Co., Oklawalia Riv., IV-10-1948, Berner, 50 MF (CAS); Okaloosa Co., Blackwater Riv., Fla. A & M Station, IV-24-1971, Peters, 32 M, 25 F (FAM); Walton Co., Black Cr. at Daniel's Fish Camp S of Hwy 294, V-1-1971, Carlson, 17 F (FAM). GEORGIA: Baker Co., Flint Riv. at Hwy 37, Newton, IX-11-1971, Carlson, 1 F (FAM); Charlton Co., 18 mi N of St. George, II-20-1954, Berner, 5 L (UF); Grady Co., Barnett's Cr. at Hwy 84, IV-15-1972, Carlson, 6 M, 5 F (FAM); Seminole Co., Lewis Lk. (Lake Seminole), VIII-29-1971, Carlson and Farmer, 75 MF (FAM); Houston Co., Tharpe's Pond 5.5 mi N of Perry, III-31-1945, Fattig, 275 MF (INHS); Bartow Co. Clear Lk, 3.5 mi N of Cassville, IV-20-1946, Fattig, 50 MF (INHS); Tift Co., Whiddons Mill Pond 6 mi NW of Chula, V-27-1946, Fatigg, 50 MF (INHS). LOUISIANA: Madison Co., Tallulah, VIII-1929, Glick, 2 F (USNM). MAINE: Hancock Co., VII-3, 5-1985, Gibbs, 8 M, 6F (all reared with exuvia), 9 L (UME); Penobscot Co., Pushaw Lake, VI-22-1986, Burian, 3 M (UME). MINNESOTA: Lake Co., Moose Lake 20 mi E of Ely, VI-17-1981, Edwards 125 MF (PERC). MISSISSIPPI: Scott Co., Roosevelt St. Pk., Morton, VIII-31-1965, Spangler, 15 M (UU); Lafayette Co., T7S-R2W-Sec. 34, V-30-1978, Stanford, 12 M, 3 F (UM); Marshall Co., Wall Doxey St. Pk., IX-9-1980, Campbell, 4 F (UM); Scott Co., Golden Mem. St. Pk., V-8-1979, Lago, 11 M, 4 F (UM); Winston Co., 13 mi W of Louisville, V-8-1980, Lago, 14 M (UM). NEW YORK: Franklin Co., Fish Creek Ponds campsite, VI-15-1976, McCafferty, et al., 8 M (PERC). NORTH CAROLINA: McDowell Co., Upper Cr., Jonas Ridge, IX-9-1967, Barrier, 1 L (CUC); Orange Co., West Fork Eno Riv. 2.1 mi S of Cedar Grove, V-5-1981, 8 L (CUC); Dare Co., Kill Devil Hills, VII-5-1950, 8 M (USNM). NOVA SCOTIA: Milford, VI-30-1934, McDunnough, 11 M. (CNC). ONTARIO: Algonquin Prov., Mew Lake, VII-8-1966, Koss, 25 M, 1 F (PERC); Leg Lake, VIII-26-1926, Osburn, 9 M (CNC). SOUTH CAROLINA: Aiken Co., Three Run Cr., VI-14,15-1977, Peters, 2 M (FAM); Anderson Co., 3 & 20 Cr. At Co Rt 115, IV-28-1977, Morse and Smith, 4 L, (CUC); Barnwell Co., Four Mile Cr., above conf. of Savannah Riv., I-10-III-16-1983, Poff, 22 L (PERC); Jasper Co., Savannah Riv. Wildlife Ref., VIII-21-1946, Upholt, 40 M, 3 F (UU); Maxwell Ponds, XI-3-1959, Skelton, 15 L. (CUC). VIRGINIA: Notloway Co., Little Nottoway Riv. 2 mi S of Crewe, VI-16-1980, Kirchner, 2 M (VPI). WISCONSIN: Iron Co., Lake of the Falls, VI-23, 24-1984, Bloodgood, 35 M, 6 F (PERC).

Caenis latipennis Banks

Caenis latipennis Banks, 1907: 14. Type Locality: Pullman, Washington. Type deposition: (M) MCZ.Caenis forcipata McDunnough, 1931: 257. Type locality: Algonquin Park, Ontario. Type deposition: (M) CNC. NEW SYNONYMY.

Caenis jocosa McDunnough, 1931: 260. Type locality: Put-in-Bay, S. Bass Isl., Ohio. Type deposition: (M) CNC. NEW SYNONYMY.

Caenis delicata Traver, 1935: 647. Type locality: Murray Co., Oklahoma. Type deposition: (M) CU. NEW SYNONYMY.

Caenis gigas Burks, 1953: 53. Type locality: Giant City State Park, Illinois. Type deposition: (M) INHS. NEW SYNONYMY.

LARVA (Fig. 3): Body length 3.0-6.8 mm.

Head.— Vertex heavily mottled with brown. Antennae pale, basal segments of flagellum usually stained light brown.

Thorax.— Pronotum usually mottled with brown; lateral margins pale, subparallel. Mesonotum usually with brown mottling, rarely uniform brown; large pale blotches laterally at wing bases, smaller pale blotches superimposed on black dashes just mediad of wing bases. Sterna pale. Legs pale; all coxae and trochanters with black dash on outer surface and small dot on mesal surface; femora with large irregular preapical black blotch often with black speckles basally; light brown band at base of tibiae and middle of tarsi; outer surface of forefemur with scattered simple setae only; inner marginal setae of mid and hind femora almost as long as outer marginal setae (Fig. 12); hind tarsus with 10-13 spurs along inner margin and ventral row of 5-7 short fimbriate spurs (Figs. 13, 14); hind tarsal claw (Fig. 24) with 11-14 denticles.

Abdomen.— Terga 1 and 2 brown on median half, pale laterally; terga 7-10 pale medially

with longitudinal sublateral brown stripes, often reduced to subtriangular blotches; terga 9 and 10 each with triad of black dots; posteromedian projection of tergum 2 acute, of moderate length (similar to Fig. 32); lateral abdominal projections of middle segments well developed, segment 5 approximately 5 times as wide as long (Fig. 41). Sternum pale; obliquely arranged pairs of black dots usually present on most sterna; posterior margin of sternum 9 truncate (Fig. 41). Operculate gills dark blackish brown, often mottled same as thorax (Fig. 3); dorsal surface with sparse, minute spiculations; both medial and apical branches of Y-ridge with long setae (similar to Fig. 48). Caudal filaments with alternating pale and light brown banding; middle portion of each filament with long lateral setae on each segment, setae much longer than spaces between them (similar to Fig. 38).

ADULT MALE (Fig. 73): Body length 2.6-4, 3 mm.

Head.— Frontal ridge edged with black; anterior area of vertex usually stained with light purplish gray; dark purplish gray transverse band between lateral ocelli, occasionally abbreviated as two lateral blotches; posterior 1/3 of vertex pale. Venter pale, with one or two pair of small black dots (Fig. 56). Antennae pale.

Thorax.— Pronotum pale, suffused with dark gray, darkest medially; margins lined with black; black submedian dashes near posterior margin. Mesonotum light amber-brown to dark chestnut-brown, anterior lateroscutellum distinctly lighter than remainder of mesonotum; black diagonal dashes at wing bases, often joining darkened border of lateroscutellum; blackish brown V-shaped mark along junction of posterior parapsidal suture; scutellum smoky. Pleura pale yellow; anteroventral area of mesopleuron same color as mesonotum; major sutures edged with black. Sternum pale. Legs pale, forefemur heavily stained with dark gray and with large black apical dash; middle and hind coxae with two black dashes on outer surface; trochanters with black dash; middle and hind femora with black preapical dash, outer surface variously suffused with black speckling (Fig. 65); tibiae with or without black speckles.

Abdomen.— Terga 1-8 heavily shaded with dark gray, posterior margins edged with black; terga 9 and 10 each with triad of black dots. Pleura 2 and 4-8 with black dashes (most pronounced on 7). Sternum pale; obliquely arranged pairs of black dots usually present on sterna 6-9 or 7-9 (similar to Fig. 70). Genital forceps (Figs. 95, 102) moderate to long, rounded, almost straight, with few microspines. Caudal filaments pale.

ADULT FEMALE: Body length 3.0-6.0 mm.

TAXONOMY: Caenis forcipata, C. jocosa, C. delicata, and C. gigas are here assigned as junior synonyms of C. latipennis.

The main characters used to separate these former species were body length, coloration, and relative genital forceps length. These characters were originally described as follows: Body lengths—*C. delicata*, 4.5 mm; *C. latipennis* and *C. forcipata*, 4.0 mm; *C. jocosa*, 3.0 mm; *C. gigas* 2.0 mm. Thoracic color—*C. latipennis*, dark brown; *C. delicata*, reddish brown; *C. forcipata*, light brown; *C. jocosa* and *C. gigas*, light yellow brown. Forceps lengths—*C. forcipata*, very long; *C. latipennis* and *C. delicata*, moderately long; *C. jocosa*, moderately short; *C. gigas*, short. My examination of collections from throughout the country showed that there are continuums in both length and coloration (especially after an examination of the types of *C. gigas* showed them to range from 2.5-2.8 mm, instead of 2.0 mm as originally described by Burks [1953]).

Caenis delicata was thought to be distinguishable from the others by the presence of black speckles on the mid and hind femora and tibiae, as opposed to speckles on the femora only.

Caenis delicata has been reported only from the Great Plains area; however, my examination of collections from throughout the country revealed that not only does the speckled leg character occur throughout the entire range of C. latipennis, but that 91% of all collections examined (containing ten or more specimens) had a mixture of speckled and non-speckled individuals. This speckling appears to be totally independent of variations in size and thoracic coloration. Two of the six specimens in the type series of C. latipennis also have speckled tibia. There is little question that this character results from normal genetic variability. A similar situation occurs in the closely related species C. punctata, which also may or may not have black speckles on the tibia.

Although the thorax of *C. forcipata* has been described as a little darker brown than *C. jocosa* and *C. gigas*, the main supposed distinguishing characteristics of these three former species were overall body length and relative genital forceps length. During the summer of 1982, the emergence of *C. latipennis* was monitored at a farm pond near the Purdue University campus. The early emergers were all fairly large, males ranging in size from 3.7-4.2 mm, typical of *C. forcipata*. As the summer progressed, individuals became smaller, passing through the 3 mm *C. jocosa* range, and ending with the smallest being only 2.7 mm, in the *C. gigas* range. Furthermore, thoracic color as well as head and abdominal patterning became lighter and less distinct as the season progressed, thus encompassing all the variations formerly assigned to different species.

Much of the apparent difference in forceps length is merely an optical illusion. The forceps of *C. forcipata*, for example, appear much larger than those of *C. gigas* because of the overall larger size of the individuals; however, when the width of the last abdominal segment vs. forceps length is compared, the true difference is only minor. Forceps lengths vs. head capsule widths were plotted for individuals from all size classes collected at the test pond as well as for individuals collected from throughout the range of the three former species (Fig. 1). Regression lines were established using the following formulas: b=y/x2 (predictive of allometry) and b=y/x (predictive of isometry). The size ratios for all individuals followed the predicted allometry line (Fig. 1), clearly showing that the relative differences in forceps length were disproportionately related to body size and resulted from allometric developmental rates, leaving little doubt that *C. forcipata*, *C. jocosa*, and *C. gigas* refer to the same species. Similar allometric genitalic differences were observed in *C. amica*. It has also been reported for *Stenonema* penes (Bednarik and McCafferty, 1979).

All specimens I examined from the far northwestern area of this species' range were typically *latipennis*-like in coloration; however, I found, as did McDunnough (1931), that many specimens from the middle Canadian Provinces and North Central States, could not be clearly assigned as either *C. latipennis* or *C. forcipata*. In addition, populations in Oregon are more *forcipata*-like in thoracic color, southward in California, they are typically *jocosa*-like, both in size and coloration. Throughout the entire range of these populations there are no clear cut demarcations between phenotypes and some latitude gradient appears to play an important role in phenotypic expression.

Caenis latipennis is obviously a highly polymorphic species. The intraspecific variation closely parallels that demonstrated in experimental work of McCafferty and Pereira (1984) to be environmentally induced in other mayflies.

The larvae of *C. latipennis* are often difficult to separate from other members of the *diminuta* group. Although the vast majority have a mottled color pattern and the majority of the other members of the group are uniform brown, this character is not consistently reliable even on a local basis and should be used with caution. The truncate 9th sternum and the

relatively uniform setal length on both the outer and inner margin of the hind femora are the only reliable characters I have found.

Adults can easily be separated by the pale posterior 1/3 of the vertex of the head and the paired ventral black spots. There is no black median line on abdominal terga 1-3 and the male forceps tend to be longer, thinner, and straighter than those of other members of the group.

Although Koss (1968) noted slight differences in the surface punctations between the eggs of *C. forcipata* and *C. jocosa*, they fall within the normal range of variability and are not indicative of species differences.

BIOLOGY AND ECOLOGY: Caenis latipennis is one of the most widespread and commonly encountered members of the genus. It is known from almost every province and state in North America, appearing to be absent only from the Rocky Mountain area and far southeastern regions of the United States (Map 4). I have a small series of females from southern Mexico which are tentatively placed as C. latipennis. The age and condition of these alcohol preserved specimens makes a positive identification difficult. Adults have a fairly long emergence period and may be encountered throughout the warmer months.

Larvae occur in almost any freshwater habitat but prefer areas with little or no current such as lakes, ponds, and the slower reaches and backwaters of rivers and streams. They inhabit a broad range of substrates including sand, mixed gravel, detritus and other debris, but show a preference for organically rich silty areas. They are often found in association with emergent vegetation. They appear to have a fairly high pollution tolerance and have occasionally been taken in sewage treatment lagoons.

MATERIAL: Paratypes, 4 M, *Caenis delicata*, OKLAHOMA: Murry Co., IV-2-1931, R. D. Bird (UU). Holotype, M, *Caenis forcipata*, ONTARIO: Algonquin Park, VI-19-?, J. McDunnough (CNC); Allotype, F. QUEBEC: Hemmingford, VII-5-?, G. H. Hammond (CNC); Paratypes, 1 M, same as Holotype (CNC), 1 M, Same as Allotype (CNC). Holotype, M, *Caenis* gigas, ILLINOIS: Giant City St. Pk., VIII-6-1946, Mohr and Sanderson (INHS); Allotype, F, same as Holotype (INHS); Paratypes, 7 M, 33 F, same as Holotype (INHS), 46 M, same as Holotype except, VII-5-1944, Sanderson and Leighton (INHS), 62 M, Hamilton, VIII-30-1931, Ross and Mohr (INHS). Holotype, MN, *Caenis* jocosa, OHIO: Put-in-Bay, S. Bass Isl., VII-10-?, C. H. Kennedy (CNC); Paratypes, 8 M, same as Holotype (CNC). Holotype, M, *Caenis latipennis*, WASHINGTON: Pullman, VI-?-?, (MCZ); Paratypes, 5 M, same as Holotype (MCZ).

Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 7836 adults, 1210 larvae). ALABAMA: Dallas Co., Cedar Cr., 5.5 mi N of Minter, VI-26, 27-1968, Peters, et al., 1 M, 8 F (FAM); Limestone Co., Wilson Lk., 25.5 mi W of Athens, VI-7-1958, Peters, 7 M, 20 F (FAM). ALBERTA: Bigoray Riv., VII-5-1973, 5 F (UU); Seven Persons Cr. nr Old Dam, Medicine Hat, VI-12-1929, Pepper, 40 L (CNC); Whitemud Cr., Edmonton, V-24-1977, Whiting, 2 L (US). ARIZONA: Douglas Co., Guadalupe Mts, Guadalupe Cany., VI-10, 11-1968, Menke and Flint, 2 F (USNM); Coconino Co., Oak Cr. Cany., VI-18-1968, Menke and Flint, 1 F (USNM). ARKANSAS: Boone Co., Bear Cr. at St Rd 14, 3 mi W of jct Hwy 281, V-28-1974, McCafferty, et al., 22 F (PERC); Fulton Co., Spring Riv. nr Hardy, VIII-24-1972, Mauney, 7 M (USNM); Saline Co., North Fork Saline Riv., 7 mi NW of Benton, VIII-15-1980, Winters, 4 M 5 F (PERC); Washington Co., Muddy Fork Illinois Riv. nr Lake Wedington, IV-28-1972, Baumann, 50 MF (USNM). CALIFORNIA: Butte Co., Horseshoe Pond, Bidwell Pk., VII-11-1970, Smith, 300 MF (FAM), Kern Co., Shafler, IV-1-1948, Van de Bosch, 8 M, 3 F, (CAS); Lake Co., Lower Lake, Cash Cr., VIII-6-1946, Chandler, 27 L (CAS); Lucerne, VII-25-1955, Leech, 20 M, 8 F

(CAS); Medera Co., Clark Pond, IV-18-1980, Gill, 26 M (FAM); Yolo Co., Davis, VIII-22-1946, Chandler, 20 L (CAS); Lake Curry, VII-9-1949, Day, 50 MF (CAS); Nice, VIII-25-1938, Lindquist, 13 M (USNM). CONNECTICUT: New Haven Co., Mt. Carmel, V-20-IX-6-1960, 8F (PMNH). ILLINOIS: Gallatin Co., Shawneetown, VII-11-1935, Mohr, 2 M (INHS); Hancock Co., Hamilton, VIII-30-1931, Ross and Mohr, 50 M (INHS); Mason Co., Havana, V-3-1984, 2 M (CNC); Union Co., Anna, V-6-1925, 2 M (CNC), INDIANA: Bartholomew Co., Haw Cr. at Columbus, VI-15-1978, Minno and Hollis, 10 F (reared with LCS), 2 L (PERC); Benton Co., Mud Cr., 2.5 mi N of Freeland Park, VIII-4-1976, Provonsha and Minno, 3 M, 5 F (reared with LCS), 17 L (PERC); Elkhart Co., Elkhart Riv., At Elkhart Riv. Preserve, Benton, VIII-2-1977, Minno and Yocum, 1 M, 6 L. (PERC); Harrison Co., Little Indian Cr. 3 mi E of Corydon, V-17-1973, McCafferty, et al., 50 MF, 18 L (PERC); Jefferson Co., Clifty Cr. nr Clifty Falls St. Pk., VI-16-1977, Provonsha, et al., 6 M, 5 F, 13 L (PERC); Knox Co., White Riv. at Cunnighams Ferry, IV-15, 16-1977, Provonsha, et al., 1 M, 2 F, 6 L (PERC); Morgan Co., Pond at Martinsville, VI-22-1983, Provonsha and Van Allen, 4 M (reared with LCS) (PERC); Tippecanoe Co., Entm. Research Area Pond, V-IX-1982, Provonsha, 4000 MF, 8 M, 14 F (reared with LCS), 150 L (PERC). IOWA: Blackhawk Co., Ceder Falls, VIII-4-1974, Knudtson, 42 M (PERC). KANSAS: Atchison Co., State Lake and Park, V-22-1978, DuBois, 4 M (PERC); Douglas Co., Reservoir Pond, West Campus, Lawrence, V-9-1977, Liechti, 50 MF (UK); Cherokee Co., Shoal Cr., 1.8 mi S of Galera, IV-28-1977, Huggins, 14 M (PERC); Clark Co., Clark Co. St. Lk., VIII-12-1975, Huggins, 32 M, 1 F (UK); Kingman Co., Kingman Co. St. Lk., V-17-1976, Liechti, 16 M (UK); Nemaha Co., Nemaha Co. St. Lk., VI-22-1977, Liechti, 2 M, 2 F (UK); Pottawatomie Co., Pottawatomie Co. St. Lk., VIII-10-1976, Oldham, 3 M, 2 F (UK); KENTUCKY: Breathitt Co., Buckhorn Cr., nr KY 976, VI-19-1978, 3 L (PERC); Breckenridge Co., Rock Lick Cr., VII-29-1980, 3 L (PERC); Christian Co., Forbes Cr. at KY 189, VIII-14-1980, 3 L. (PERC); Clark Co., Lulbegrud Cr., 3.8 km SE of Rightangle, VII-25-1983, 14 L (PERC); Fleming Co., Sand Lick Cr. at rd to Mt Vernon Cem., XI-7-1983, 9 L (PERC). MAINE: Kennebec Co., W. Gard, VI-21-1975, Dill, 3 M (PERC); Piscataquis Co., Moosehead Lake, VII-29-1986, Burian, 18 M (UME). MANITOBA: Victoria Beach, Lake Winnipeg, VII-19-?, Wallis, 4 F (CNC). MARYLAND: Frederick Co., Potomac Riv., VI-16-1973, Richardson, 1 L (ANSP); Montgomery Co., Potomac Riv., Point of Rocks, VI-21-1960, Roback, 1 L (ANSP). MEXICO: Chiapas State, Tab. Rio Chacama, Palenque, XII-6-1975, Menke and Flint, 1 M, 5 F (USNM). MICHIGAN: Benzie Co., Platte Riv., Honor, V-27-1939, Frison and Ross, 45 MF (INHS); Berrien Co., Grand Mere Lakes, V-20-66, Donahue, 8 M, 10 F (PERC); Chippewa Co., Mouth of Tubquamenon Riv., 5 mi S of Paradise, VII-24-1966, Roback, 3 M (ANSP); Ottawa Co., Black Riv., Holland, VI-18-1939, Steggerda, 1 M (INHS). MINNE-SOTA: Jackson Co., Lilen Woods St. Pk., VII-9-16-1972, 2 M (UMSP); Lake Co., Moose Lk., 20 mi E of Ely, VI-17-1981, Edwards, 30 MF (PERC); West Branch Beaver Riv., VI-28-1978, Ekmann, 4 L (UMSP); Ramsey Co., Pond nr Snelling Ave., & Lake Johanna Blvd., V-6-1976, Wickstrom, 14 L (UMSP); Stern Co., St. Cloud, VII-7-1931, Yeager, 75 MF (UMSP) Wabasha Co., Lake City, VIII-6-1935, Gurney, 16 M (UMSP). MISSISSIPPI: Calhoun Co., T11S-R3W-Sec 25, VII-12-1978, Stanford, 4 F (UM); Jasper Co., 6 mi NW of Montrose, V-7-1980, Lago, 50 MF (UM); Neshoba Co., 4 mi N of Dixon, V-9-1979, Lago, 27 MF (UM); Newton Co., 6 mi SE of Newton, V-10-1979, Lago, 1 M (UM); Rankin Co., 10 mi NE of Canton, V-6-1980, Lago, 4 M, 6 F (UM). MONTANA: Carter Co., Box Elder Cr., VI-26-1974, Roemhild, 9 L. (MTSU); same, V-30-1977, 50 MF (MTSU); Daniels Co., W. Fk. Poplar Riv., VII-17-1979, Roemhild, 15 L (MTSU); Fallon Co., Sandstone Cr., VI-27-1974,

Roemhild, 20 L (MTSU); Phillips Co., Nelson Riv., VI-1-1977, Roemhild, 13 M, 3 F (MTSU); Wibaux Co., Beaver Cr., V-31-1975, Roemhild, 16 L (MTSU). MISSOURI: Ozark Co., Mammoth Springs, VI-6-1937, Ross, 1 M, 1 F (INHS). NEBRASKA: Box Butte Co., Niobrara Riv., Hwy 2-71, V-20-1980, Carnevalo, 3 L (UNO); Chase Co., Champion Lake, V-22-1979, Decker, 5 L (UNO); Cherry Co., Sparks, VII-10-16-1977, 1M (UNL); Dawes Co., pond at Chadron St. College, VI-15-1984, McCafferty and Provonsha, 2 F (PERC); Furnas Co., Republican Riv., S of Oxford, VIII-31-1980, Decker, 8 L (UNO); Hitchcock Co., Frenchman Riv., S of Calbertson, V-19-1980, Decker, 4L (UNO); Holt Co., VI-1974, 16 M, 12 F, 3 L (UNL); Lincoln Co., Jeffery Res., V-20-1979, Decker, 18 L (UNO); Sherman Co., Middle Loup Riv., .5 mi W of Loup City, VIII-17-1979, Decker, 2 L (UNO). NEW BRUNSWICK: Fredericton, VII-20-1924, Brown, 3 M, 2 F (CNC). NEW YORK: Tompkins Co., Ithaca, VII-25-1914, 27 M (CNC); Chautauqua Co., Canada Way Cr., SE of Fredonia, VII-9-1975, Peters, 1 M, 5 F (FAM). NORTH CAROLINA: Orange Co., Eno Riv., VI-10-1981, 2 L (SWRC). NORTH DAKOTA; Pembina Co., T16N-R56W-Sec. 22, VI-24-1975, Lago, 1 F(UM); Slope Co., Burning Coal Vein, VIII-15-1975, Lago, 1 M(UM). OHIO: Ottawa Co., Lake Erie, Put-in-Bay, VII-7, 8-1975, Peters, 2 M, 1 F (FAM); same, VIII-24-1937, Mohr, 27 M (PERC); Putnam Co., Auglaize Riv. below jct with Ottawa Riv., S of Cloverdale, VII-5-1956, Roback, 3 L (ANSP). OKLAHOMA: Delaware Co., Flint Cr., VI-6-1973, Stark, 2 F (UU); Latimer Co., Red Oak Cr., 5 mi SE of Red Oak, VI-7-1973, Stark, 2 M, 7 F (UU); Murry Co., IV-2-1931, Bird, 15 M, 10 F (UU); Ottawa Co., Fivemile Cr., 5.1 mi N, 1.25 mi E of Peoria, VI-9-1983, Liechti, et al., 3 L (PERC); McCurtain Co., Mt. Fork Riv., Hochatown, VI-8-1940, Weddle, 6 M, 13 F (INHS). ONTARIO: Greens Cr., VI-1-1928, Adams, 6 L (CNC); Lake Nipigon, VIII-5-1923, 2 M, 1 F (CNC). OREGON: Benton., S of Corvallis, VIII-16-1934, Gray and Schuh, 15 M, 10 F (UU); Douglas Co., Fish Lk., VIII-14-1958, Alexander, 1 F (UU); Klamath Co., Klamath Falls, VI-26-1977, Schuh, 15 M (FAM); Lake of Woods, Rogue Riv., Nat'l Forest, VI-27-1962, Toschi, 27 M (UCB); Lane Co., Reerslev Farm, 2 mi S of Ferguson, VIII-9-1976, 10 M (US); Polk Co., VII-5-1980, Harper, 2 M, 1 F (US). PENNSYLVANIA: Clinton Co., Kettle Cr., VI-30-1938, Wetzel, 1 M (INHS); Brandford Co., Susquehanna Riv., Athens, VIII-5-1937, Eddleson, 11 M (INHA); Butler Co., Wolf Cr., 1.5 mi NW of Slippery Rock, IX-1-1967, Roback 8 L (ANSP); Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, VI-1-1981, Roback, 3 L (SWRC). QUEBEC: Alymer, VII-20-1924, Curran, 31 M (CNC); Lac Attila, Baie James, VIII-3-1973, 2 M (CEUM); Lapeche Riv., Wakefield, VI-9-1930, McDunnough, 10 L (CNC); Misstassini Post, VII-21-1956, Lonsuby, 50 MF (CNC). SASKATCHEWAN; Atton's Lake, VI-10-1940, 37 M, (CNC); Waskesiu Lake, VII-20-1939, Brooks 34 M (CNC); Battle Riv. at Hwy 13 nr Consul, V-23-1974, Smith and Dosdall, 12 L (US); Nemieben Lk., VI-23-1977, Mason, 6 M (US). TENNESSEE: Sullivan Co., Holston Riv., VI-28-1974, Roback, 1 L (ANSP); Sumner Co., Cumberland Riv., IX-11-1973, Richardson, 2 L (ANSP). TEXAS: Austin Co., Brazos Riv. At Austin St. Hist. Pk., V-9-1977, McCafferty, et al., 1 M (PERC); Jasper Co., Neches Riv., at US Hwy 69, V-4-1977, McCafferty, et al., 4 M (PERC); La Salle Co., Cotulla, IV-15-17-1928, Pratt, 2 F (CNC); Palo Pinto Co., Palo Pinta, IV-27-1939, Ross, 150 MF (PERC); Webb Co., Laredo, XI-18-1939, Berner, 8 M (UU). VIRGINIA: Fairfax Co., Bull Run., Rt 28, VIII-13-1980, Kondratieff, 4 F (VPI); Rockingham Co., South Fork Shenandoah Riv., Goods Mill, V-26-1971, Surber, 8 M (VPI); Washington Co., North Fork Holston Riv., Mendola, VI-7-1979, Hoffmon, 1 F (VPI). WASHINGTON: Spokane Co., Latah Cr., Spokane, VIII-1-1967, Edmunds, 1 F (UU); Whitman Co., Pullman, VII-11-1898, 2 M (CNC). WEST VIRGINIA: Pendleton Co., Grandy Cr. nr spruce Knob, VI-22-1973, Stark, 17 M (UU). WISCONSIN: Iron Co., Lake of the Falls, VI-24-1984, Bloodgood, 12 M, 10 F (PERC); Monroe Co., Squaw Lake, Ft. McCoy, VIII-6-1981, Provonsha, 50 MF, 13 L (PERC); Vilas Co., Trout Lake, VI-7-10-1939, Nelson, 33 M, 6 F (INHS); Walworth Co., Bigfoot Beach St. Pk., VI-20-1957, 24 M (PERC). WYOMING: Platte Co., 10 mi N of Wheatland on US Hwy 87, VI-7-1961, Edmunds and Peters, 1 M, 7 F (UU); Sweetwater Co., Black's Fork Riv., at I-80, W of Green River City, VII-18-1968, Koss, 1 M, 1 F (PERC).

Caenis punctata McDunnough

Caenis punctata McDunnough, 1931: 259. Type locality: Hemmingford, Quebec, Canada. Type deposition: (M) CNC.

LARVA: Body length 4.0-6.0 mm.

Head.— Medium brown, dark brown surrounding lateral ocelli and at posterolateral corners; pale spot usually present anterior to median ocelli. Antennae pale.

Thorax.— Pronotum light brown medially, graded to dark brown laterally; pair of submedian black dots near posterior margin; lateral margins pale, subparallel. Mesonotum usually uniform brown, occasionally mottled; large pale blotches anteromedially and laterad of wing bases; short black dashes congruent with small pale spots just mesad of wing bases. Sterna pale, with pair of small submedian black dots on metasternum between hind coxae. Legs pale; coxae and trochanters with black dash on outer surface; femora with large preapical V-shaped black dash, usually surrounded by wide brown band encircling femora; mid and hind femora usually with black speckling on dorsal (outside) surface near base (most pronounced on hind femur); all tibiae and tarsi with prebasal brown band; dorsal surface of forefemur with scattered simple and occasionally bifurcate setae (similar to Fig. 9); inner marginal setae of mid and hind femora much shorter than outer marginal setae (similar to Fig. 10); hind tarsus with row of 12-14 spurs along inner margins and ventral row of 6-8 fimbriate spurs (similar to Figs. 11, 14); hind tarsal claw with 18-22 denticles, basal 4-6 denticles larger than apical denticles (Fig. 25).

Abdomen.— Tergum pale medially, brown laterally; terga 9 and 10 each with triad of small black dots; posteromedian projection of tergum 2 moderately long, hook shaped in lateral view, broadly triangular in dorsal view (similar to Fig. 32); posterolateral projections of middle segments well developed, segment 5 approximately 5.5-6.0 times as wide as long (similar to Fig. 40). Sternum pale; sterna 2-7 with longitudinal black dashes at base of lateral projections forming an abbreviated longitudinal stripe; sterna 5-9 or 6-9 usually with 2 pair of obliquely arranged submedian black dots, anterior segments with single pair of black dots; posterior margin of sternum 9 rounded (similar to Fig. 40). Operculate gills uniform brown; dorsal surface with sparse, minute spicules (as in Fig. 88); medial and apical branches of Y-ridge with long setae (similar to Fig. 48). Caudal filaments with alternating pale and brown banding; middle portion of filaments with long lateral setae on each segment, setae much longer space between them (similar to Fig. 38).

ADULT MALE (Fig. 74): Body length 2.8-4.4 mm.

Head.— Vertex entirely shaded with blackish purple darkest in posterior half, pair of small submedian black dots anterior to transverse arms of epicranial suture; second pair just ventrad of frontal ridge; venter with irregular black transverse band between compound eyes (similar to Fig. 54). Vestigial mouthparts narrowly bordered with black. Antennae pale.

Thorax.— Pronotum pale yellow, heavily shaded with smoky, darkest medially and

anterolaterally; margins with strong black borders. Mesonotum yellowish brown; lateral margins and anterolateral scutum pale yellow, black transverse dash at wing bases; narrow black V-shaped stripe along base of posterior parapsidal suture; scutellum smoky. Pleura yellowish brown with smoky shading anteriorly, pale yellow posteriorly, dorsal margin anterior to wings and anterior margin black; all primary sutures black. Sterna pale; submedian black dots on metasternum between hind coxae. Legs pale, all coxae and trochanters with black streak on outer surface; forefemur smoky, preapical black spot fairly large, forming a band partially encircling femur; middle and hind femora (Fig. 66) with sprinkling of black dots; black preapical dash V-shaped, often extending ventrally forming a partial or often complete band encircling femora; occasionally traces of median band (especially on middle femur); mid and hind tibia occasionally with black speckles.

Abdomen.— Median area of terga 1 and 2 with indistinct black medial line, lateral margins suffused with dark gray; terga 3-6 uniformly shaded with dark gray; dark gray sublateral blotches on terga 7-9 becoming progressively smaller, often totally lacking on 9; terga 9 and 10 with triads of black dots; median dot on 10 often elongated into short longitudinal dash. Pleura pale with black dashes on 1-9, strongest on 7 (often indistinct on 3 and 9). Sternum pale; pairs of obliquely arranged sublateral dots usually present on most sterna (similar to Fig. 70). Genital forceps (Figs. 96, 103) short, stocky, moderately covered with microspines. Caudal filaments pale.

ADULT FEMALE: Body length 3.6-5.0 mm.

TAXONOMY: Larvae of *C. punctata* are difficult to separate from those of *C. amica* and *C. diminuta*, which also have a rounded 9th sternum. The larvae can be distinguished from *C. amica* by the number of size of the hind tarsal claw denticles. *Caenis amica* has 9-11 denticles of uniform length or becoming progressively larger toward the tip of the claw. *Caenis punctata* has 18-22 denticles with a basal 4-6 denticles larger than the apical denticles. The differences in adult leg markings are usually also visible on the larvae. The number of fimbriate spurs on the ventral surface of the hind tarsus will separate *C. punctata* from *C. diminuta*. *C. punctata* possesses 6-8 fimbriate spurs and *C. diminuta* has 9-11. The thoracic coloration of *C. punctata* is usually somewhat lighter than *C. diminuta* and the antennal scape is always pale on *C. punctata* and usually darkened on *C. diminuta*. These color characters, however, must be used with caution.

The band encircling the mid and hind femora on fully pigmented adults will readily distinguish them from adults of all other species except *C. diminuta*. The totally pale antennal scape and pedicel and the presence of black speckles on the mid and hind femora will consistently separate adults of *C. punctata* from adults of *C. diminuta*. On lighter individuals, the femoral band may be greatly abbreviated or absent, closely resembling the femora of *C. amica*. The submedian black spots on the anterior region of the vertex and just ventrad of the frontal ridge of the head; the V-shaped black preapical spot (as opposed to a triangular spot); and the very short, stocky male forceps of *C. punctata* will readily separate lighter individuals from *C. amica*.

BIOLOGY AND ECOLOGY: Although it may be locally abundant, *C. punctata* has been reported from only scattered localities through the eastern half of the United States and Canada (Map 5). It has not been previously reported from the far Southeast. But, reexamination of collections labeled *C. diminuta* from Mississippi, Florida, and the Carolinas revealed a small percentage of *C. punctata*.

The majority of larval collections are from lentic habitats with sand or fine gravel substrates. The adult emergence period is from early May through August in the northern

portion of its range and extends through November in the South.

MATERIAL: Holotype, M, QUEBEC: Hemmingford, VII-15-?, G. H. Hammond (CNC); Allotype, F, same as Holotype (CNC); Paratypes, 7 M, same as Holotype (CNC). Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 683 adults, 87 larvae). ARKANSAS: Saline Co., North Fork Saline Riv. 7 mi NW of Benton, VIII-15-1980, Robison and Winters, 6 M, 2 F (SAU). CONNECTICUT: New Haven Co., Mt. Carmel, V-20-IX-6-1960, 2 F (PMNH). FLORIDA: Calhoun Co., Chipola Riv., Hwy 71, IX-12-1972, Carlson, 200 MF (FAM); Gulf Co., Dead Lake, Hwy 71, 4 mi N of Wewahtichka, X-29-1971, Carlson, 36 MF (FAM); Liberty Co., Apalachicola Riv., Hwy 20 at Bristol, IV-29-1972, Carlson, 16 M (FAM). INDIANA: Crawford Co., Stinking Fk. Blue Riv., at St Rd 66, 1 mi S of Sulfur Springs, V-18-1978, Provonsha, Bloodgood, 1 F (PERC); Monroe Co., Bryant's Lake, Morgan-Monroe St. For., VIII-19-1981, 1 F (PERC); Morgan Co., Pond at Hwy 39, Martinsville, VI-17-1974, Provonsha, 11 M, 4 F (PERC); same, VII-8-1983, Provonsha, M. Doub, 2 M (reared with LCS), 25 L (PERC); Posey Co., Wabash Riv. at Old Dam, New Harmony, VIII-12-1974, Provonsha and Dersch, 1 F (PERC); Ripley Co., Versailles Lake, Versailles St. Pk., VII-18-1972, Provonsha, 2 M (PERC); Spencer Co., Pond 0.5 mi W of Pigeon Cr. at Hwy 62, VI-14-1983, Provonsha and Van Allen, 15 M, 7 F, (4 M, 4 F reared with LCS), 14 L (PERC); Warren Co., Little Pine Cr. At Highbridge, V-31-1973, Provonsha and Black 1 M, 1 F, (PERC). KANSAS: Chautauqua Co., Old Sedar City Lake, VI-6-1978, Hamilton, 1 M (PERC). MAINE: Penobscot Co., Penobscot Riv., at Winn, VIII-7-1980, Tsomides, 1 M. (UME). MISSISSIPPI: Bolivar Co., 2 mi S. Rosedale, XI-3-1980, Lago, 14 M, 1 F (UM); Hancock Co., 6 mi WNW of Waveland, V-26-1980, Lago, 25 MF, (UM); Jasper Co., 6 mi NW of Montrose, V-7-1980. Lago, 10 M, 7 F, (UM); Marion Co., Lake Columbia, IV-21-1979, Lago, 4 F (UM); Marshall Co., Wall Doxey St. Pk., IX-9-1980, Campbell, 2 M, 1 F (UM); Rankin Co., 10 mi NE of Canton, V-6-1980, Lago, 1 F (UM). NEW YORK: Franklin Co., Fish Cr. Ponds Campsite, VI-15-1976, McCafferty, et al., 2 M (PERC). NORTH CAROLINA: Iredell Co., trib. of West Fk. Rocky Riv., at Mt. Mourne, V-31-1981, 1 M (DPC). OKLAHOMA: Latimer Co., Turkey Cr. 6 mi E of Red Oak, VI-5-1973, Stark, 14 M, 2 F (UU). ONTARIO: Algonquin Prov., Park, Mew Lake, VII-8-1966, Koss, 1 F (PERC). SOUTH CAROLINA: Barnwell Co., Steel Cr. Swamp, IV-25-1984, B. Kondratieff, 1 M, 4 F (PERC); Greenville Co., Saluda Riv., 12 mi E of Betton, VI-7-1981, 1 M (DPC); Newberry Co., Saluda Riv., Buzzard Roost Hdro. Sta., VI-25-1981, 9 M (DPC). TENNES-SEE: Dickson Co., Lake in Montgomery Bell Pk., V-27-1954, Edwards, 4 F (UU). TEXAS: Jasper Co., Neches Riv. at US Hwy 69, V-4-1977, McCafferty, et al., 6M, 1 F (PERC). VIRGINIA: Craig Co., John's Cr., Rt 311, VI-30-1978, Kondratieff, 5 F (VPI); Fairfar Co., Bull Run, Rt 28, VIII-13-1980, Kondratieff, 1 M, 1 F (VPI); Fauquier Co., Broad Run, Throughfare Gap, VII-26-1975, Flint, 2 F (USNM). WISCONSIN: Vilas Co., Trout Lake, VII-10-1937, Nelson, 2 M (INHS).

Caenis youngi Roemhild

Caenis youngi Roemhild, 1984: 7. Type locality: Madison Arm of Hebgen Lake, Gallatin Co., Montana. Type deposition: (M) USNM.

LARVA: Body length 4.8-6.3 mm.

Head.— Vertex uniform light to medium brown. Antennae pale; basal 2-4 segments of

flagellum usually stained with tan.

Thorax.— Pronotum light to medium brown; black submedian spots near posterior margin; lateral margins pale, straight, and strongly divergent anteriorly, anterior margin extending beyond compound eye a distance equal to width of lateral ocelli (Fig. 8). Mesonotum light to medium brown; large pale spots and black transverse dashes at wing bases. Sterna light yellow-tan. Legs pale; irregular black subapical dash on all femora; light brown band near base of all tibiae and trochanters; dorsal surface of forefemur with scattered setae only (similar to Fig. 9); inner marginal setae of mid and hind femora much shorter than outer marginal setae (similar to Fig. 10); inner margin of hind tarsus lined with 12-14 spurs; ventral surface with row of 9-11 fimbriate spurs (similar to Figs. 11, 14); hind tarsal claw (Fig. 26) with 18-21 moderately sized denticles.

Abdomen.— Terga 1 and 2 light brown with dark brown sublateral blotches; terga 7-10 uniform light brown with blackish brown blotches laterally; terga 9 and 10 each with triad of black dots; posteromedian projection of tergum 2 long, rounded apically in lateral view, truncate in dorsal view (Fig. 33); posterolateral projections of middle segments 5 approximately 5 times as wide as long (similar to Fig. 40). Sternum pale yellowish white; 2 pair of obliquely arranged submedian black spots on most sterna; posterior margin of sternum 9 rounded (similar to Fig. 40). Operculate gills uniform blackish brown; dorsal surface with sparse, minute spicules (similar to Fig. 88); medial and apical branches of Y-ridge with long setae (similar to Fig. 48). Caudal filaments pale with light brown distal bank on each segment; middle portion of each filament with long lateral setae on each segment, setae much longer than space between them (similar to Fig. 38).

ADULT MALE (Fig. 75): Body length 4.2-4.8 mm.

Head.— Vertex completely shaded with smoky black, darkest posterior to transverse arm of epicranial suture. Venter with irregular black transverse band between compound eyes (similar to Fig. 54). Antennae pale; base of pedicel and flagellum darkened.

Thorax.— Pronotum pale, heavily marked with black, Mesonotum dark brown; prescutum black; all sutures black; scutellum smoky, edged with black. Pleura pale dorsally, dark bronzy brown ventrally; anterior margin blackish brown. Sterna yellowish tan. Forecoxa, trochanter, and femur heavily stained with dark smoky brown; dark brown annulation near base of tibia; mid and hind legs pale; coxae and trochanters with narrow black line on outer surface; femora with black preapical dash.

Abdomen.— Terga 1 and 2 pale medially with black median line, dark gray laterally; terga 3-7 heavily shaded with dark gray; terga 9 and 10 with triads of black dots (median dot on tergum 10 often elongated into a short dash); posteromedian margin of tergum 2 with fleshy, finger-like projection (Fig. 61). Pleurum pale; black dots and 1 and 3-9, most prominent of segment 7. Sternum pale; sterna 1-5 or 1-6 with single pair of black submedian dots, 6-9 or 7-9 with 2 pair of obliquely arranged dots; dark gray median blotches often present. Genital forceps (Fig. 104) moderately long, rounded, slightly bowed, with few microspines. Caudal filaments pale.

ADULT FEMALE: Body length 5.8-6.2 mm.

TAXONOMY: Caenis youngi was described by Roemhild in 1984, making it one of the most recent North American species of Caenis to be described. Roemhild included descriptions and illustrations of both the adult and larva.

Although the larvae are similar in general coloration to those of other species in the *diminuta* group, they are morphologically distinct. The anteriorly divergent margins of the pronotum together with the greatly enlarged, upwardly directed projection on abdominal

segment 2 readily distinguishes them from all other known larvae.

Adults are similar in coloration to *C. amica*. The fleshy finger-like projection on abdominal segment 2 is the main distinguishing character. Females and male subimagos also frequently retain vestiges of the expanded larval pronotum. Within the *diminuta* group, a well developed projection on abdominal segment 2 is shared only by *C. candida* which is totally devoid of all leg and abdominal color markings. There is a possibility that *C. youngi* is the dark phase of *C. candida*; however, at this time there is insufficient evidence to form a definite conclusion.

BIOLOGY AND ECOLOGY: Caenis youngi appears to have a northern distribution and may eventually be found to occur throughout much of Canada. At present it is known only from Montana, the Yellowstone and Grand Teton areas of Wyoming, Alberta, and the upper peninsula of Michigan (Map 2). Larval collections are from lakes and small, slow moving streams with sandy substrates. The Montana and Wyoming sites are from altitudes between 1900-2100 m, far higher than any previously known North American Caenis habitat. All adult records are from July.

MATERIAL: Paratypes, 2 M, MONTANA: Gallatin Co., Hebgen Lake, Whiskey Bay, VIII-20-1982, G. Roemhild (PERC); Paratype, 1 F, same (MTSU).

ALBERTA: Parkland Co., Clifford E. Lee Nature Sanct., VI-19-1979, Corkum, 13 L (UW); Trib. entering Buffalo Lk. 52 deg. 27' N, 113 deg. 18' W, VI-15-1978, Corkum, 2L (UW); Rosebud Cr. 51 deg. 40' N, 114 deg. 06' W, VI-13,1979, Corkum, 5L (VPIVP). MICHIGAN: Marquette Co., Ives Lake, VII-9-11-1985, McCafferty and Provonsha, 39 MF, 15 L (PERC). MONTANA: Beaver Head Co., Hidden Lake, VII-5-1979, Roemhild, 1 F (MTSU); Cascade Co., W of Simms, VIII-4-1975, Roemhild, 1 L (MTSU); Gallatin Co., Hebgen Lake, Wiskey Bay, VIII-20-1982, Roemhild, 7 F (MTSU); Hebgen Lake, West Yellowstone, VII-19-1983, Waltz, 10 M, 1 F (PERC); Lake Co., Lake Many Ronan, VII-13-1975, Roemhild, 11 L (MTSU); same, Flathead Lake, Yellow Bay, VIII-10-1964, Nebeker, 4 M, 1 F (UU). WYOMING: Teton Co., Valley Floor, Grand Teton Nat'l. Pk., VI-29-1983, Gulley, 1 L (PERC); Garnet Canyon, Grand Teton Nat'l. Pk., VI-20-1982, Gulley, 2 L (PERC); Yellowstone Nat'l. Pk., Slough Cr., VII-7-1982, Roemhild, 1 L (MTSU).

Hilaris Group

LARVA: Forefemur with transverse row of spatulate (often appearing bifurcate) setae (Figs. 15, 18, 19, 82, 83); mid and hind tarsi with 0-2 fimbriate spurs on ventral surface near apex (Fig. 17); posterior margin of sternum 9 notched (Figs. 42-44).

Overall, in this group, the body tends to be narrower, the lateral abdominal projections less pronounced, and the tarsal claw denticles generally smaller and fewer in number than compared to the *diminuta* group.

ADULTS: Wing vein ICuA1 forked with CuA2 distad of CuA1-CuP crossvein (Fig. 59); marginal wing setae extend beyond radial sector, usually reaching wing tip; male forceps short, flattened, both shaft and tip densely covered with microspines (Figs. 105-110).

EGGS: Usually with 1 (rarely 2) Type I polar cap (Figs. 112-115).

In general, this group is smaller in size than the *diminuta* group, males ranging from 2.0-3.2 mm. Thew (1960) designated a "hilaris complex" to include all North American and several European species. His grouping should not be confused with the hilaris group as here defined.

BIOLOGY AND ECOLOGY: Larvae of the hilaris group are found primarily in lotic

habitats with slow to moderate currents. They occur on a broad range of substrates such as fine sand, gravel, logs, and other debris.

Although the emergence period will vary with local conditions, the voltinism appears to be more uniform than with those in the *diminuta* group. All species for which I have been able to obtain data are bivoltine with midsummer and early fall emergences.

Caenis anceps Traver

Caenis anceps Traver, 1935: 645. Type locality: Varna, New York. Type deposition: (M) CU.

LARVA (Fig. 4): Body length 2.6-3.8 mm.

Head.— Anterior vertex brown, small pale spot anterior of median ocelli; area posterior of transverse arm of epicranial suture light tan, narrow dark brown stripe transversing head between lateral ocelli. Antennae light tan.

Thorax.— Pronotum brown with paired submedian black dots; lateral margins pale, subparallel. Mesonotum brown; black dashes near anterolateral margins, at wing bases, and along posterior parapsidal sutures; indistinct pale spots at wing bases. Sterna light tan. Foreleg with basal 3/4 of femur pale, apical 1/4 diffusely shaded with light brown surrounding small black subapical spot; dorsal (outside) surface lightly spiculate, with irregular transverse row of spatulate setae (Fig. 19); mid and hind legs pale, preapical femoral spot absent; hind tarsus with marginal row of 4-6 short spurs restricted to apical 1/2 and 0-2 fimbriate spurs on ventral surface near apex; hind tarsal claw with 4-6 minute denticles (Fig. 27).

Abdomen.— Terga 1 and 2 tan; terga 7-10 uniform brown or tan medially, graded to brown laterally; posteromedian projection of abdominal tergum 2 short, broadly triangular in dorsal view (Fig. 34); posterolateral projections of middle abdominal segments moderately developed, segment 5 approximately 4.5 times as wide as long (Fig. 42). Sternum tan; posterior margin of sternum 9 moderately notched (Fig. 42). Operculate gills tan anteriorly between fork of Y-ridge, graded to brown posteriorly (Fig. 4); dorsal surface densely covered with moderately large, stout spicules (Fig. 89); medial branch of Y-ridge with 4-6 stout bifurcate setae. Caudal filaments tan; middle portion with whorls of short setae on every 2nd or 3rd segment, setae shorter than space between whorls (Fig. 39).

ADULT MALE: (Fig. 76): Body length 2.0-2.8 mm.

Head.— Vertex whitish, anterior and posterior margins narrowly bordered with black; purplish black stripe transversing head between lateral ocelli. Antennae pale.

Thorax.— Pronotum pale, with darker shading laterally; black dashes near anterolateral margins; two black submedian dots on posterior margin. Mesonotum medium red-brown to orange-brown; scutellum tinged with smoky black. Pleura yellow-brown, medium red-brown anteroventrally. Sterna pale yellow. Forefemur pale basally and dark brown apically; foretibia usually purplish black at base; mid and hind legs entirely pale with preapical black spot on femora small and indistinct or totally absent.

Abdomen.— Entirely pale, somewhat yellow-tinged apically. Forceps short, flattened, densely covered with microspines (Figs. 97, 105, 106). Caudal filaments pale.

ADULT FEMALE: Body length 2.6-3.4 mm.

TAXONOMY: Hagen (1861) designated two specimens as types of C. amica, but only one of them corresponds to the original description. Hagen had also noted that the second specimen was somewhat different from the first and possibly represented a different species.

This other specimen is actually C. anceps.

The larva of *C. anceps* is distinguished from other members of the *hilaris* group by the short projection on abdominal tergum 2 and the graded coloration of the operculate gills, and the whorls of short setae on the caudal filaments (shared only with the unplaced species *C. bajaensis*).

Adults are distinguished by the dark transverse bar between the lateral ocelli; the reddish brown thorax; and the lack of markings on the mid and hind femora and on the abdominal terga.

As with other members of the *hilaris* group, the eggs (first described by Koss, 1968) have a Type I polar cap. Although there is normally only one such cap, some females have been found with a mix of single- and double-capped eggs. Both kinds of eggs also exist in *C. hilaris* and the South American species *C. cuniana* (Froelich, 1969).

BIOLOGY AND ECOLOGY: Caenis anceps ranges through most of eastern North America (Map 6). Adult records are from July through September. Larvae are rarely found in lakes and ponds. The vast majority of collections examined were from flowing water habitats with clean sand or fine gravel substrates. In Indiana, it appears to be bivoltine, with major emergences in mid July and early to mid September.

MATERIAL: Paratypes, 5 M, 1 F, NEW YORK: Varna, VII-15-1931, J. R. Traver (CNC). Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 1680 adults, 275 larvae). ARKANSAS: Clay Co., Current Riv. nr Missouri St. Ln., VI-5-1977, 8 L (ASU); Clebourne Co., Beech Fork, E of Woodrow, VIII-11-1979, 6 L (ASU); Montgomery Co., Ouachita Riv. at Rocky Shoals Boat Camp, US Hwy 270, VI-1-1974, McCafferty, et al., 1 M, 1 L (PERC); same Little Missouri Riv., IX-10-1980, Bacon, 9 L (PERC); Van Buren Co., South Fork Little Red Riv., at St Hwy 95, XII-18-1979, 1 L (ASU); Yell Co., Arkansas Riv., Dardanelle, VIII-8-1957, Peters and Eberhart, 12 M, 93 F (FAM). ILLINOIS: Kane Co. Aurora, VII-17-1927, 3 F (CNC); Vermilion Co., Oakwood, VII-10-1927, 2 F (CNC). INDIANA: Elkhart Co., Elkhart Riv. At Elkhart Riv. Preserve, Benton, VIII-2-1977, Minno and Yocum, 18 M, 12 F, 19 L (PERC); LaGrange Co., Pigeon Riv. at 525 E, Pigeon Riv. Fish and Game Area, VIII-27-1975, Provonsha, 35 M, 18 F (PERC); Pulaski Co., Tippecanoe Riv. 1.5 mi S of Tippecanoe St. Pk. VII-30-1976, Provonsha and Minno, 25 M, 6 F (PERC); Wayne Co., Greens Fork Whitewater Riv., 3 mi S of Greens Fork, VIII-27-1974, Provonsha and Dersch, 43 L (PERC); White Co., Tippecanoe Riv. at Hwy 18, Springboro, VII-28-1984, Provonsha and Bloodgood, 34 M, 27 F (6 M, 4 F, reared), 6 L (PERC); IOWA: Linn Co., Cedar Rapids, IX-5-51, Edmunds, 8 M, 1 F (UU). KENTUCKY: Marion Co., Rolling Fork, 2 km NE of Jessietown, VIII-4-1983, 54 L (PERC); Rockcastle Co., Dix Riv. nr Copper Cr. Rd. bridge, VII-27-1983, 300 L (PERC); Taylor Co., Robinson Cr. at Mannsville, VII-27-1983, 20 L (PERC). MAINE: Kennebec Co., Kennebec Riv., 2 mi below Hinckley, VIII-12-1975, Richardson, 4 L (ANSP). MARYLAND: Frederick Co., Potomic Riv., 3/4 mi above US Hwy 15, VI-16-1973, Richardson, 3 L (ANSP); Montgomery Co., Potomic Riv. At Whites Ferry, VI-18-1956, Roback, 1 L (ANSP). MINNESOTA: Lake Co., Bear Lake, VI-28-1975, 2 L (UMSP); Pine Co., Snake Riv., VI-12-1977, 36 L (UMSP). MISSOURI: Christian Co., Finley Cr. 1 mi W of Linden, IX-10-1979, Sullivan, 21 M, 8 F, 7 L (PERC). NEW YORK: Montgomery Co., Canajoharie, VII-12-1934, Townes, 25 M, 12 F (UMSP); Tomkins Co., Ithaca, VII-6-1934, Townes, 4 M (UU). OKLAHOMA: Latimer Co., Turkey Cr. 6 mi E of Red Oak, VI-5-1973, Stark, 1 M (UU). PENNSYLVANIA: Chester Co., Pickering Cr. 1.3 mi WNW of Charlestown below Rd 15046, VI-19-1989, 8 L (SWRC); Wyoming Co., Meshoppen Cr. 1.6 mi E Meshoppen, VII-21-1980, 2 L (SWRC). TENNES- SEE: Campbell Co., VI, Berner, 21 M, 6 F (UF). VIRGINIA: Bath Co., Jackson Riv., Rt 603, Richaidson's Gorge, IX-11-1979, Kondratieff, 24 M (VPI); Floyd Co., Little Riv., Rt 615, VII-18-1978, Kondratieff, 32 F (VPI); Giles Co. Rt 635, VI-4-1977, Powell, 25 M, 200 F (VPI); Montgomery Co., Little Riv., Rt 787, VIII-5-1980, Kondratieff, 29 M, 5 F (VPI); Smyth Co., South Fork Holston Riv., jct Rts 660-600, VIII-13-1979, Voshell, 40 M, 12 F (VPI); Washington Co., Holston Riv. below Rt 91 bridge, VI-26-1974, Roback, 10 L, (ANSP). WEST VIRGINIA: Pendleton Co., Franklin, VIII-17-1938, Musgrave, 23 M, 4 F (UU).

Caenis hilaris (Say)

Ephemera hilaris Say, 1939: 43. Type locality; Indiana. Type deposition: (M) Unknown. Caenis hilaris, Eaton, 1884: 147.

LARVA (Fig. 5): Body length 2.7-4.0 mm.

Head.— Vertex brown with large pale spots surrounding median and lateral ocelli and median arm of epicranial suture. Antennae pale.

Thorax.— Pronotum brown, lateral margins pale, subparallel; pale submedian spots and pale posteromedian spot usually visible; two submedian black dots or dashes near posterior margin. Mesonotum brown with large pale spots; black streaks near anterolateral margins, near wing bases, and along posterior parapsidal sutures. Sternum pale. Legs pale; all femora with black preapical dash; light brown banding at midlength of tibiae and near base of tarsi often visible; forefemur (Fig. 15, 82) with transverse row of spatulate setae (Fig. 16, 83) on dorsal (outside) surface; hind tarsus with 6-9 spurs along inner margins and 0-2 fimbriate spurs on ventral surface near apex (Fig. 17); hind claw (Fig. 28) with 5-6 small denticles.

Abdomen.— Tergum 1 mostly pale brown; tergum 2 brown on median 2/3, pale laterally; black spots near anterolateral margins; tergum 7-9 pale medially, brown laterally, black dashes usually visible near lateral margins; tergum 10 pale anteriorly, brown on posterior 2/3; posteromedian projection of tergum 2 moderately long, broadly triangular in dorsal view (Fig. 35); posterolateral projections of middle abdominal segments moderately developed, segment 5 approximately 4 times as wide as long (Fig. 43). Sternum pale; occasionally with sublateral tan blotches on anterior sterna; posterior margin of sternum 9 moderately notched (Fig. 43). Operculate gills with distinct but somewhat variable pattern of brown and white (usually as in Fig. 5, occasionally as in Fig. 50 or Fig. 51); dorsal surface with overlapping, shingle-like spiculations (Fig. 90); Y-ridge usually marked with dark brown and forked at or slightly apical of midlength of gill; medial branch with 5-7 stout setae (Fig. 49). Caudal filaments pale, middle portion of each filament with long lateral setae on every segment, setae much longer than space between them (similar to Fig. 38).

ADULT MALE (Fig. 77): Body length 2.0-3.0 mm.

Head.— Vertex white, usually unmarked, occasionally with light purplish gray shading near lateral ocelli and/or on anterior half of vertex. Antennae pale.

Thorax.— Pronotum whitish; anterolateral margins usually tinged with black; two submedian black dots near posterior margin. Mesonotum pale yellow; prescutum, black; short transverse black dashes at wing bases; smoky gray V-shaped mark at juncture of posterior parapsidal sutures; scutellum tinged with smoky gray. Pleura pale with blackish streaks at bases of legs, wings, and along primary sutures. Sterna pale. Legs white; coxae with prominent black spot on outer surface; femora with a short black preapical dash (Fig. 67).

Abdomen.— White; terga 1 and 2 shaded with smoky gray; black dashes usually present along pleural margins of segments 2 and/or 7-9 only; Sternum white, unmarked. Genital forceps (Figs. 98, 107) short, flattened, densely covered with microspines. Caudal filaments pale.

ADULT FEMALE: Body length 2.5-3.8 mm.

Similarly marked as male, but shading on head often more pronounced; occasionally with sublateral smoky gray blotches on terga 1-6.

TAXONOMY: This species was originally described by Say (1839) as *Ephemera hilaris*. The type locality was cited only as "Indiana". It is assumed that they were collected at the Wabash River near his home in New Harmony, Posey County. Unfortunately, the type specimens have been lost or destroyed.

Smith (1935) described and figured the eggs of what he thought was *C. hilaris*. This was undoubtedly a misidentification as both the description and figure of the eggs fit representatives of the *diminuta* group, and not *C. hilaris*.

Caenis hilaris has one of the most distinctly patterned larva of any North American Caenis. The brown and white markings on the operculate gills and the pale median portion of the abdomen will usually separate it from other species. Darker specimens, on which the pale area of the operculate gills is greatly abbreviated, may be confused with C. tardata which has uniformly brown gills. The number of spurs on the hind tarsus and the location of the operculate gill Y-ridge fork and the number of setae on the medial branch will consistently separate C. hilaris from C. tardata. The developing black spots near the lateral margins of abdominal segments 7-9 are usually visible on the larvae of C. hilaris, whereas they are always absent on C. tardata.

Adults can usually be identified by the presence of black pleural dots on abdominal segments 2 and/or 7-9 only. Lighter specimens, however, may totally lack these pleural markings as well as the black apical dot on the middle and hind femora. Such individuals have often been misidentified as *Amercaenis ridens* (= C. ridens). *Amercaenis ridens* possesses a distinct finger-like projection on abdominal tergum 2, which is totally absent on C. hilaris.

The adult head of *C. hilaris* is usually totally pale, but may occasionally be tinged with light purplish shading between the lateral ocelli. This shading is most pronounced in populations from the mountainous regions of Arkansas on which the shading extends forward to the frontal ridge. Females in this population often possess sublateral smoky gray blotches on the anterior terga and except for the presence of black pleural spots on abdominal segments 7-9, closely resemble *C. tardata*.

In addition to the difference in head and abdominal markings, the majority of females from mountainous Arkansas contain eggs with two polar caps instead of the usual single cap. Of the females examined, the majority contained all double-capped eggs, with a few containing a mixture of both single- and double-capped eggs. I have also examined females from Virginia and Alabama that contained a small percentage of double-capped eggs. This variable egg character also exists in *C. anceps* and the South American species, *C. cuniana* (Froelick, 1969).

BIOLOGY AND ECOLOGY: Caenis hilaris ranges throughout most of the eastern United States (Map 8). Berner (1950) reported C. hilaris from Florida. Adult records are from early June through September. In Indiana, it appears to be bivoltine, with major emergences in early July and early September. The larvae appear to be restricted to flowing water and are most frequently encountered in areas of moderate current. They are the dominant Caenis in many larger midwestern rivers. Substrate preferences range from clean, fine sand to mixed

gravel, but they are also often found on submerged logs and other debris.

MATERIAL: Specimens listed below were selected to indicate general range and seasonal occurrence (total examined: 3269 adults, 417 larvae). ALABAMA: Bibb Co., Berner, 200 MF, (UF); Dallas Co., Cedar Cr., 5.5 mi N of Minter, VI-26, 27-1968, Peters, et al., 50 M, 65 F (FAM); Escambia Co., Conecuh Riv., S of Pollard, IV-28-1967, Peters, 9 L (FAM); Perry Co. Cahaloa Riv., St Hwy 183, VI-1-1968, Peters 75 M, 30 F, 2 L (FAM). ARKANSAS: Boone Co., Bear Cr., St Rd 14, V-28-1974, McCafferty, et al., 25 M, 55 F (PERC); Bradley Co., Saline Riv., IX-21-1976, Bacon, 9 L (PERC); Drew Co., Saline Riv., Ozment's Bluff, X-21-1980, Bacon, 11 M, 16 F (PERC); Montgomery Co., Ouachita Riv., Rocky Shoals Boat Camp at US Hwy 270, VI-1-1974, McCafferty, et al., 20 M, 15 F, 4 L (PERC); Scott Co., Mill Cr., Y-City, VI-29-1980, Robinson, 125 MF (PERC). GEORGIA: Baker Co., Flint Riv. at hwy 37, Newton, IX-11-1971, Carlson, 1 F (FAM); Chickasawhatchee Riv., at hwy 37, 10 mi W of Newton, IX -11-1971, Carlson, IM, 1 F (FAM). ILLINOIS: Henderson Co., Oquawka, IX-20, 26-1947, Ross, 50 MF (INHS); Iroquis Co., Wellington, VIII-6-1947, Banks and Jard, 200 MF (INHS); Kankakee Co., Kankakee, VIII-16-1938, Ross and Burks, 5 M, 5 F (INHS); Ogle Co., Oregon, VII-18-1927, 43 M, 2 F (PERC); Pike Co., Mississippi Riv., Jackson Is. opp. Hannibal, MO, IX-6-1940, 13 M (INHS); Pope Co., VII-8-1967, 3 M, 35 F (UU); Tazewell Co., Mackinaw Riv., Mackinaw, VII-4-1939, Johnson, 3 M (INHS). INDIANA: Lawrence Co., Spring Mill St. Pk., VI-20-1972, Provonsha, 104 F (PERC); Martin Co., East Fork White Riv. at Hindostan Falls Pub. Fish. Site, VII-26-1977, Minno and Yocum, 40 M, 23 F (PERC); Pulaski Co., Tippecanoe Riv. 1.5 mi S of Tippecanoe Riv. St. Pk., VII-30-1976, Provonsha and Minno, 11 M, 1 F, 12 L (PERC); Posey Co., Wabash Riv. at Old Dam, New Harmony, VIII-12-1974, Provonsha and Dersch, 140 MF (PERC); White Co., Tippecanoe Riv. at Springboro, VI-VIII-1984, Provonsha and Bloodgood, 800 MF, 14 L (PERC). IOWA: Story Co., Ames, VII-22-1928, Walley, 5 M (CNC). KANSAS: Atchison Co., Atchison Co. St. Lk., VIII-10-1978, DuBois, 8 F (UK); Clay Co., Douglas Co., Lawrence, VIII-17-1930, Brown, 4 M, 7 F (PERC); Mitchell Co., Solomon Riv. below dam at Beloit, VIII-4-1977, Roth, 30 M, 20 F (UK); Neosho Co., Neosho Riv. 2.3 mi W of St Paul at Hwy K-57, X-1-1978, Liechti, 11 F (UK); Shawnee Co., Kansas Riv. nr Lecompton, IX-19-1958, Roback, 1 L (ANSP). KENTUCKY: Johnson Co., Jenny Cr. at KY 825, VI-28-1978, 15 L (PERC); Lewis Co., Kinniconick Cr., 0.4 km ESE of KY 344-377 jct, VII-22-1983, 23 L (PERC); Taylor Co., Robinson Cr. at Mannsville, VII-27-1983, 3 L (PERC). MARY-LAND: Frederick Co., Potomac Riv. at Putonold, IX-21-1971, Roback 2 L (ANSP); Montgomery Co., Potomac Riv. 4 mi below mouth of Monocacy Riv., IX-8-1963, Roback, 2 L (ANSP). MISSISSIPPI: Lafayette Co., T75-R2W-Sec. 25, IX-26-1977, Zuccaro, 1 M, 1 F (UM); Itawamba Co., Berner, 4 M, 4 F, 12 L (UF); Wilkinson Co., Buffalo Riv. at Hwy 61, V-27-1980, Lago, 12 F (UM). MISSOURI: Christian Co., Finley Cr., 1 mi W of Linden, IX-10-1979, 1 M, (PERC); Clay Co., Missouri Riv., Riverside, VIII-4-1958, Peters, 18 M, 24 F (FAM). NEBRASKA: Cherry Co., VII-11-1977, Pruess, 2 L (UNL); Furnas Co., Republican Riv., S of Oxford, VIII-11-1982, Provonsha and Van Allen, 6 M, 4 F (reared with LCS), 18 L (PERC); Platte Co., Columbus, VII-2-1940, Hamilton, 1 F (CAS). OKLAHOMA: Ottawa Co., Fivemile Cr 5.1 mi N, 1.25 mi E of Peoria, VI-9-1983, Liechti, et al., 2 L (PERC). SOUTH CAROLINA: Barnwell Co., Steel Cr. Swamp, X-4-1984, B. Kondratieff, 1 M (PERC); Greenville Co., Saluda Riv., Holidays Bridge Hydro. Sta., 12 mi E of Belton, VI-7-1981, 50 MF (DPC); Newberry Co., Saluda Riv., Buzzard Roost Hydro. Sta., VI-25-1981, 9 M, 5 F (DPC). TENNESSEE: Davidson Co., Cumberland Riv. 1.25 mi below Hills Is., X-6-1983, Richardson 4 L (ANSP); Sumner Co., Cumberland Riv., 1 1/4 mi upstream from Old Hickory Lock and Dam, IX-12-1973, Richardson 1 L (ANSP). TEXAS: Austin Co., San Bernard Riv. at I-10 nr Sealy, V-9-1977, McCafferty, et al., 2 M, 1 F (reared with LCS) (PERC); Victoria Co., Guadalupe Riv. nr Victoria, VIII-21-1962, Roback, 1 L (ANSP). VIRGINIA: Fairfax Co, Bull Run, VIII-13-1980, Kondratieff, 12 M, 29 F (VPI); Hanover Co., South Anna Riv., Rt 657, IX-11-1978, Kondrotieff, 70 MF (VPI); Montgomery Co., New Riv., McCoy, VIII-28-1976, Bailey, 1 M (VPI). WISCONSIN: Onieda Co., Squaw lake, VII-4-1974, Harris, 1 M (PERC).

Caenis macafferti new species

Caenis amica, Traver, 1935: 645.

LARVA: (Fig. 6): Body length 3.0-4.4 mm.

Head.— Vertex dark brown; large pale spot anterior to median ocelli; black transverse line bordering posterior margin of transverse arm of epicranial suture. Antennae light brown.

Thorax.— Pronotum medium brown with pair of submedian black dots; lateral margins pale, subparallel. Mesonotum medium brown with no distinct pale markings; indistinct black dashes at anterolateral margins, near wing bases, and in scutal area. Sterna tan. Legs pale; all femora with subapical black spot, dorsal (outside) surface heavily spiculate. Forefemur (Fig. 18) with transverse row of spatulate setae on dorsal surface; hind tarsus with 9-11 marginal spurs; hind claw with 6-8 small denticles (Fig. 29).

Abdomen.— Terga 1 and 2 light brown with pale lateral margins; terga 7-10 uniform light brown; posteromedian projection of tergum 2 narrowly triangular in dorsal view, approximately twice as long as wide (Fig. 36); posterolateral projections of middle abdominal segments moderately developed, segment 5 approximately 4 times as wide as long (Fig. 44). Sternum tan; apical sterna often diffusely shaded with brown; posterior margin of sternum 9 slightly notched, often approaching truncate (Fig. 44). Operculate gills uniform brown; dorsal surface densely covered with elongate spicules (Fig. 91); medial and occasionally apical branch of Y-ridge with long bifurcate setae (Fig. 52). Caudal filaments uniformly tan; middle portion of each filament with long lateral setae on every segment, setae longer than space between them (Similar to Fig. 38).

ADULT MALE (Fig. 78): Body length 2.2-3.2 mm.

Head.— Vertex uniformly shaded with fulvous black; venter light fulvous. Antennal scape and pedicel tan.

Thorax.— Pronotum shaded with fulvous black, only slightly lighter than head; margins narrowly black; pair of black anterolateral transverse dashes and posterior submedian dots. Mesonotum brassy fulvous; prescutum and median notal suture black; scutellum smoky. Pleura light brassy fulvous. Sterna light brassy fulvous. Legs lightly shaded with smoky fulvous; forefemur dark brown anteriorly; preapical dash on mid and hind femora large but poorly defined (Fig. 68).

Abdomen.— All terga heavily shaded with light fulvous-black; pleura 1-6 with black spots, black longitudinal dashes on 7-9; posterior margin of tergum 10 surrounding bases of cerci black; tergum 2 with long, fleshy, finger-like posteromedian projection (Fig. 62). Sternum faintly smoky; indistinct darker sublateral spots occasionally visible on posterior sterna. Sternum 9 fulvous, distinctly contrasting with pale sub-genital plate. Genital forceps (Fig. 108) tan, short, densely covered with microspines. Caudal filaments pale.

ADULT FEMALE: Body length 3.0-4.0 mm.

TAXONOMY: Traver (1935) described what she considered the adults of *C. amica* from numerous specimens collected along the east coast of the U.S., although, to my knowledge, she had not seen Hagen's types of that species. Since that time, her concept of the species has persisted. What Traver assumed was *C. amica* is in reality a species, here named *C. macafferti*.

The combined characters of uniformly brown abdominal terga and operculate gills, a long narrowly triangular projection on abdominal segment 2, and long lateral setae on the caudal filaments will separate *C. macafferti* larvae from all other members of the the *hilaris* group. *Caenis anceps* larvae closely resemble those of *C. macafferti* in general color, but have a very small projection on abdominal tergum 2 and lack long lateral setae on the caudal filaments.

The combined characters of a completely shaded head, heavily shaded abdomen, black dots on the pleura, and the finger-like projection on abdominal tergum 2, will separate *C. macafferti* adults.

BIOLOGY AND ECOLOGY: Caenis macafferti is predominantly an eastern species occurring from the Appalachians eastward and from New York in the North to Florida in the South (Map 9). The only known exception is its occurrence in the mountainous regions of northwestern Arkansas. This distribution pattern is also shared by several other Appalachian mayfly species (McCafferty and Provonsha, 1978).

The majority of collections I have examined are from small to moderately sized, clear-water rivers and streams with gravelly substrates; however, larvae may occasionally be found in lakes and ponds. Adult records are from early June through mid October. Emergence apparently occurs during both the early evening and early morning hours.

ETYMOLOGY: Phenetic spelling of McCafferty. Named in honor of W. Patrick McCafferty who has contributed significantly to our knowledge of the Ephemeroptera in general and assisted greatly with this *Caenis* study.

HOLOTYPE: (M) SOUTH CAROLINA: Aiken Co., Upper Three Run Cr. at SRL, VI-14/15-1977, W. L. and J. G. Peters (PERC).

PARATYPES: (All deposited at PERC except when noted) 53 M, 14 F, 68 MS, 9 FS, same data as holotype; 2 M, 21 MS, 3 FS, Savannah Riv. Plant, Upper Three Run Cr. at SRP "F", VII-22-1977, Herlong and Prichard (CU); 1 L, Savannah Riv. Plant, Upper Three Run Cr. at SRP 8-1, XI-6-1976, Herlong and Prichard (CU); 4 MS, same data as above except, VII-8-1977, (CU); 2 L, same data as above except, VIII-22-1977, (CU); 4 L, Savannah Riv. Plant, Boggy Gut Cr. at SRP 781-4, X-16-1976, Herlong and Prichard (CU); 2 L, same data as above except, VI-1-1977 (CU); 1 L, Savannah Riv. Plant, Tinker Cr. at SRP 8-1, IX-18-1976 (CU); 1 L, same data as above except, VI-1-1977 (CU); 1 L, Savannah Riv. Plant, Mill Cr. at SRP E-2, XI-6-1976, Herlong and Prichard (CU); 8 L (parts on slides), same data as above except, VI-1-1977 (CU); 1 M, 117 MS, 1 FS, same data as above except, VI-13-1977 (CU); 2 L, same data as above except, VI-28-1977 (CU); 25 L (parts on slides), Barnwell Co., Savannah Riv. Plant, Mill Cr. at 33 deg. 19 min. N, 81 deg. 35 min, W, IX-19-1976, Herlong and Prichard (CU); 7 L, same data as above except, VII-22-1977 (CU).

OTHER MATERIAL EXAMINED: ARKANSAS: Scott Co., Mill Cr. at Y-City, VI-29-1980, Robison, 9 M (PERC). FLORIDA: Calhoun Co., Chipola Riv. at Hwy 20, IV-20-1972, Carlson, 500 MF (FAM); Desoto Co., Nocatee Peace Riv., VIII-4-1950, 25 L (UF); Liberty Co., Sweetwater Cr., VI-4-1938, Berner, 14 L (UF). GEORGIA: Cherokee Co., Etowah Riv., 6.5 mi ESE of Ball Ground, VI-22-1971, Peters, et al., 25 L (FAM). NEW YORK: Delaware Co., Delaware Riv., Hancock, VII-22-1935, Townes, 3 M, 3 F (UMSP). PENNYSLVANIA:

Bedford Co., Big Otter Riv., Co Rd 670, VII-2-1980, Parrish, 3 L (SWRC); Chester Co., East Fork White Clay Cr., VII-22-1970, Richardson, 1 F (reared with LCS); same VII-16-1982, 9 L (SWRC). SOUTH CAROLINA: Aiken Co., Upper Three Runs Cr., X-21-1984, B. Kindratieff, 50 MF (PERC); Anderson Co., Old Fish Hatchery, IX-23-1961, O'Brien, 1 L (CUC); Newberry Co., 5 mi SSE of Whitmire, V-J 19-1981, 3 L (SWRC); Oconee Co., Little Riv. at Salem, IX-3-1975, Nichols, 4 L (CUC); Pickens Co., Maxwell Ponds, Clemson, X-3-1959, Schroeder, 8 L (CUC). VIRGINIA: Buckingham Co., Slate Riv. 5 mi W of Mt. Rush, VI-11-1981, Pierson, 5 L (SWRC); Fauquier Co., Thumb Run, 1.15 mi NW of Orlean, VI-12-1981, Pierson, 5 L (SWRC); Rappahannock Co., Thornton Riv., 6.2 mi S of Ben Venue, VI-11-1980, 12 L (SWRC); Rockbridge Co., Bark Veg., GR5K, VIII-30-1977, Meschiter, 1 M (VPI).

Caenis tardata McDunnough

Caenis tardata McDunnough, 1931: 260. Type locality: Lethbridge, Alberta, Canada. Type deposition: (M) CNC.

LARVA: Body length 3.0-4.5 mm.

Head.— Vertex medium brown with dark brown sinuous lines; large pale area surrounding median arm of epicranial suture; areas adjacent to ocelli pale. Antennal scape and pedicel pale, flagellum tan.

Thorax.— Pronotum medium brown, diffuse pale submedian blotches usually visible; lateral margins pale, subparallel. Mesonotum medium brown; large diffuse pale blotches at wing bases; small pale spots superimposed on black diagonal dashes medial to wing bases. Sterna light tan. Legs pale; forefemur with diffuse light brown apical band encompassing black subapical spot; mid and hind femora usually with diffuse light brown along ventral and apical margins and with black subapical spot; mid and hind tibiae light brown on basal 1/2; forefemur with transverse row of spatulate setae on dorsal (outside) surface (similar to Fig. 15); hind tarsus with 11-13 spurs along inner margin and 0-1 fimbriate spur on ventral surface near apex; hind tarsal claw with 5-8 small denticles (Fig. 30).

Abdomen.— Terga 1 and 2 medium brown, lateral margins pale; terga 7-9 pale medially and laterally, with distinct brown longitudinal sublateral stripes; tergum 10 brown; posteromedian projection of tergum 2 triangular, of moderate length (similar to Fig. 35); posterolateral projections of middle segments moderately produced, segment 5 approximately 4 times as wide as long (similar to Fig. 43). Sternum tan, large sublateral brown blotches usually present on most sterna; posterior margin of sternum 9 moderately notched (similar to Fig. 43). Operculate gills uniform brown; dorsal surface densely covered with elongate spicules (similar to Fig. 91); Y-ridge forked distad of mid length of gill, medial branch with 10-12 setae (Fig. 53). Caudal filaments uniform tan; each segment in middle portion of filaments with long lateral setae, setae much longer than space between them (similar to Fig. 38).

ADULT MALE (Fig. 79): Body length 2.0-2.6 mm.

Head.— Vertex extensively shaded with fulvous black, usually darkest just posterior to transverse arm of epicranial suture. Antennae pale.

Thorax.— Pronotum pale, tinged with smoky gray; traces of narrow black lines along anterolateral and posterior margins; pair of submedian black dots or dashes near posterior margin. Mesonotum light to medium chestnut brown, usually darkest along median suture;

all primary sutures faintly marked with black; black transverse dashes at wing bases; tip of scutellum smoky black. Pleura pale yellow dorsally, medium to dark brown ventrally; primary sutures black. Sterna pale yellow, often lightly tinged with brown. Forecoxa heavily shaded with blackish brown; foretrochanter and femur smoky with distinct subapical black streak. Mid and hind legs pale; coxae with large black spot on outer surface; femora with narrow preapical streak (similar to Fig. 67), often indistinct.

Abdomen.— Terga 1-6 pale medially; broad longitudinal smoky gray stripes near lateral margins; most pronounced on anterior segments; terga 7 and 8 entirely pale; faint smoky shading on 9 and 10, a small black median dot usually visible on 9. Pleurum pale, unmarked. Sterna 1-8 pale, unmarked; sternum 9 pale yellow, posterior margin often bordered by narrow smoky gray line. Genital forceps (Figs. 109, 110) short, flattened, densely covered with microspines and distinct sensory setae. Caudal filaments pale.

ADULT FEMALE: Body length 3.0-3.8 mm.

Longitudinal blackish blotches on abdominal terga usually broader and darker than in males.

TAXONOMY: The uniformly brown operculate gills and longitudinal brown stripes on the abdomen will usually distinguish the larvae of *C. tardata* from others of the *hilaris* group. They may occasionally be confused with *C. anceps*, *C. macafferti* or *C. hilaris* on the bases of color alone. The caudal filament setae of *C. anceps* larvae are arranged in short whirls. The posteromedian projection on abdominal tergum 2 of *C. macafferti* larvae is much longer than on *C. tardata*. Darker individuals of *C. hilaris*, on which the white patterning on the operculate gills is greatly reduced, may be confused with *C. tardata*. The number of spurs on the hind tibia in combination with the location of the operculate gill Y-ridge fork and the number of setae on the medial branch will consistently separate *C. tardata* from *C. hilaris*.

The extensive shading on the head in combination with the laterally oriented longitudinal blackish blotches on an otherwise pale abdomen distinguish the adults. On lighter individuals, however, the abdominal markings may be greatly reduced, being only slightly visible on the anterior segments. Such adults have often been misidentified as *C. anceps*, which has a totally pale abdomen. The western populations (Alberta, Manitoba, Montana, Minnesota, and Nebraska) typically possess a transverse band on the head just posterior to the transverse arm of the epicranial suture which is much darker than the remainder of the vertex. In the eastern populations (Indiana, West Virginia, and Virginia), the vertex of the head is uniform gray. In addition, thoracic color is lighter and the sublateral blotches on the abdominal terga are much less pronounced than in the western populations.

Day (1956) reported *C. tardata* from California; however, specimens identified by him that I have examined are all *C. bajaensis*.

BIOLOGY AND ECOLOGY: This is one of the less commonly taken *Caenis* in North America. It has been reported from scattered localities throughout the eastern and central United States and central Canada (Map 10). It was erroneously reported from California by Day (1956). Like other members of the *hilaris* group, the larvae of *C. tardata* are found primarily in larger rivers with substrates ranging from fine sand to mixed gravel. Adult records range from June through September.

MATERIAL: Holotype, M, ALBERTA: Lethbridge, VIII-5-?, J. H. Pepper (CNC); Allotype, F, same as Holotype (CNC); Paratypes, 15 M, same as Holotype (CNC).

Specimens listed below were selected to indicate general ranges and seasonal occurrence (total examined: 348 adults, 62 larvae). ALBERTA: Milk Riv., IX-13-?, Pepper, 3 M (CNC). INDIANA: LaGrange Co., Pigeon Riv. Wildlife Area, VIII-25-1975, Provonsha, 18 M, 4 L

(PERC); Pulaski Co., Tippecanoe Riv. 1.5 mi S of Tippecanoe Riv. St. Pk., VI-30-1978, Provonsha, et al., 50 MF (PERC); Starke Co., Robins Ditch at jct Hwys 30-35, VII-14-1976, Provonsha and Minno, 1 M, 4 F (reared, with LCS), 10 L (PERC). MINNESOTA: Clay Co., Buffalo Riv. St. Pk., VIII-24-1971, Baker, 4 M, 4 F (UM). MONTANA: Phillips Co., irrigation canal at Malta, VII-4-1977, Roemhild, 25 M, F (MTSU). NEBRASKA: Dundy Co., South Fork Republican Riv., 3 mi S of Benkelman, Decker, 4 L (UNO); Furnas Co., Republican Riv., S of Oxford, VI-17-1980, Decker, 4 L (UNO); same, VIII-11-1982, Provonsha and Van Allen, 1 M, 3 F, 6 L (PERC); Hitchcock Co., Republican Riv. 1/4 mi S of Stratton, VI-16-1980, Decker, 12 L (UNO); Holt Co., VI-1974, Pruess, 100 MF (UNL); Merrick Co., Platte Riv. 15 mi W of Osceola, Hwy 92, VIII-17-1979, Decker, 3 L (UNO); Sheridan Co., Niobrara Riv. at St Rd 27, VI-16-1984, McCafferty and Provonsha, 23 L (PERC); Sherman Co., Middle Loup Riv. 1/2 mi W of Loup City, Hwy 92, VIII-17-1979, Decker 2 L (UNO); Webster Co., Republican Riv. S of Red Cloud at Hwy 281, VI-18-1980, Decker, 3 L (UNO). SASKATCHEWAN: Indian Head, VII-29-1925, deGryse, 1 M (CAS); N. Saskatchewan Riv., Cecil Ferry, 10 mi E of Prince Albert, VII-13-1981, Lehmkuhl, 28 M, 4 L (US). VIRGINIA: Augusta Co., Middle Riv., Mt. Meridian, IX-22-1978, Seagle, 24 M (VPI); Shenandoah Co., North Fork Shenandoah Riv., Mavertown, IX-21-1971, Surber, 15 M (VPI); Warren Co., South Fork Shenandoah Riv., Front Royal Public Boat Landing, IX-21-1978, Seagle, 21 M (VPI). WEST VIRGINIA: Hampshire Co., Cacapon Riv., Rt 50, VII-16-1980, Kondratieff, 50 MF (VPI).

Unplaced to Group

Caenis bajaensis is not placed in either the diminuta or the hilaris group at this time. It has characters common to both groups. However, other characters such as the shape of the tarsal claws and the large number of claw denticles, the deeply cleft 9th sternum, the broadly based median projection on tergum 2, and the chisel shaped apices of the male genital forceps are unique and may indicate that this southwestern species was independently derived.

Caenis bajaensis Allen and Murvosh

Caenis bajaensis Allen and Murvosh, 1983: 431. Type locality: Stream, Rd. to Comondu, Baja California Sur. Type deposition: (L) CAS.

LARVA (Fig. 7): Body length 4.0-5.0 mm.

Head.— Vertex dark brown in anterior half; posterior half often tan with dark brown reticulations; large pale spot anterior of median ocelli. Antennae pale.

Thorax.— Pronotum brown with darker reticulations and large paler sublateral blotches; lateral margins pale, subparallel. Mesonotum uniform brown, often paler along inner margin of wing pads; short black transverse dashes at wing bases. Sterna pale, often stained with light purplish brown medially. Legs pale; femora lightly stained apically with smoky black; forefemur (Fig. 20) with transverse row of spatulate setae; hind tarsus (Fig. 21) with 8-10 simple marginal spurs and ventral row of 8-10 fimbriate spurs (Fig. 84); hind tarsal claw with 20-25 minute denticles (Fig. 31).

Abdomen.— Tergum uniform brown, posterior margin of tergum 2 broadly expanded, posteromedian projection broadly based, moderately long, triangular (Fig. 37); lateral abdominal projections of middle segments well developed, segment 5 approximately 5.5-6.0

times as wide as long (Fig. 45). Sternum pale, with blackish lateral blotches; blackish median blotches often present; posterior margin of sternum 9 deeply notched (Fig. 45). Operculate gills uniform brown; dorsal surface densely covered with short, stout spicules (similar to Fig. 89); medial and usually apical branches of Y-ridge with long setae. Caudal filaments pale; middle portion of each filament with whorls of short setae on every 2nd or 3rd segment, setae much shorter than space between whorls (similar to Fig. 39).

ADULT MALE (Fig. 80): Body length 2.5-3.8 mm.

Head.— Vertex uniformly shaded with dark fulvous black; venter with pair of submedian black dots. Antennal scape and pedicel stained with tan; base of flagellum blackish.

Thorax.— Pronotum fulvous black medially, pale laterally; lateral and posterior margins edged with black. Mesonotum medium orange-brown to dark chestnut-brown, prescutum, all sutures and scutellum with fulvous black markings. Pleura pale fulvous; dorsal area of episternum anterior to wing bases diffusely shaded with fulvous black, coxal cavities ringed with black. Sterna tan. All coxae lightly shaded with fulvous; all femora with diffuse fulvous apically, often extending longitudinally along entire upper margin; no distinct black subapical spot; foretibia and all tarsi pale; mid and hind tibia light fulvous black. Wing vein ICuA1 forked with CuA2 just distad of CuA1-CuP crossvein (Fig. 60); marginal setae not extending beyond medial sector.

Abdomen.— All terga heavily shaded with fulvous black. Dorsum of pleura 1-6 pale, 7-9 edged with black. Sternum light tan; black diagonal dashes at lateral margins of most sterna, often extending onto venter of pleura. Anterior margin of subgenital plate with short black lateral transverse dashes and fulvous black median spot. Genital forceps (Figs. 99, 111) tan, relatively short, flattened, somewhat chisel shaped at tip, densely covered with microspines basally, becoming sparse apically. Caudal filaments pale to light tan.

ADULT FEMALE: Body length 3.0-4.0 mm.

EGGS: With two Type II polar caps.

TAXONOMY: The existence of an undescribed species of *Caenis* in California was first suspected by Day (1956). Although he briefly described the adult male, the species was not named. My examination of his material showed it to be what was subsequently described by Allen and Murvosh (1983) as *C. bajaensis*. The larvae of *C. bajaensis* are easily separated from all other North American species by the large number of minute denticles (20-25) on the hind tarsal claw, the expanded posterior margin of tergum 2, and the deeply notched 9th sternum. Several other characters are common to either the *diminuta* or *hilaris* group, but are not found in combination in any other species. These include a row of fimbriate spurs on the mid and hind tarsi (common to all species in the *diminuta* group); a diagonal row of bifurcate setae on the forefemur (common to the *hilaris* group); and whorls of short setae on the caudal filaments and the form of the spicules on the dorsum of the operculate gills (shared only by *C. anceps* of the *hilaris* group).

The combined characters of a heavily pigmented head and abdomen with no black pleural spots, forked CuA1-CuA2 wing veins, chisel shaped apices of the densely microspined male forceps, and the two type II polar caps on the eggs distinguish the adults. As with the larvae, adults possess characters common to both the *diminuta* and *hilaris* groups. The forked CuA1-CuA2 wing veins and the flattened, densely microspined male forceps resemble those of the *hilaris* group. The reduced wing marginal setae and the two Type II polar caps on the eggs are shared in common with the *diminuta* group.

I have in my possession adult *Caenis* from Argentina that closely resemble *C. bajaensis*. Unfortunately, I have no associated larvae, nor have I seen any Mesoamerican or South

American larvae that resemble *C. bajaensis*. I have, however, seen larvae from Africa that are very close to it in all respects.

BIOLOGY AND ECOLOGY: Caenis bajaensis occurs throughout Mexico and the southwestern United States (Map 10). The Pine Ridge area of northwestern Nebraska is the furthest north and east that it has been taken. Adult emergence ranges from June through September in the United States and extends through December in Mexico. Larvae have been collected from sandy bottomed streams with slow to moderate currents. They have not been taken in association with any other Caenis species.

MATERIAL: Holotype, L, BAJA CALIFORNIA SUR: Stream, Rd. to Comondu, V-29-1979, Allen and Murvosh (CAS); Paratypes, 5 L, same data as holotype (CAS); 1 L, Rio Poza, 5.2 mi (8.4 km) SW Loreto, Rd. to San Javier, Allen and Murvosh (CAS).

Specimens listed below were selected to indicate general ranges and seasonal occurrence (total examined: 246 adults, 112 larvae). ARIZONA: Cochise Co., Chirichua Mts., 5 mi W of Portal, VIII-12-1952, Leech and Green, 7 MF, 8 L (PERC). Coconino Co., West Fork Oak Cr. at 1st crossing, 0.25 mi above jct. W/Oak Cr. Cany., V-6-1981, Brigham, Brigham and Sanderson 4 L (PERC); Greenlee Co., Middle Fk. Black Riv., Apache Nat'l Forest, VI-23-1977, Tarzwell, 9 L (PERC); Santa Cruz Co., Yanks Spring, VIII-12-1952, Leech and Green, 42 M (CAS); Madera Cany., V-7-1969, Koss and Provonsha, 3 L (PERC); Yavapai Co., Oak Cr. Cany., VI-18-1968, Flint and Menke (USNM); Creek in Hull Cany., 2 mi W of Jerome at old copper mine on US 89A, V-5-1981, Brigham, Brigham and Sanderson, 14 L (PERC). CALIFORNIA: Fresno Co., Kings Riv., IX-8-1978, Gill, 22 M (FAM); Napa Co., Sage Cr., IV-22-1950, Day, 2 M, 1 L (CAS); Stanislaus Co., Patterson, Adobe Cr., V-9-1948, Day, 1 L (CAS). COLORADO: Clear Creek Co., Berthoud Pass, VIII-19-1949, Harmston, 3 M (UU). MEXICO: Chiapas State Tab., Rio Chaemax, Palenque, XII-6-1975, Flint, 2 F (USNM); Durango State, Las Adjuntas, VI-30-1952, Lattin, 23 M (UCB); same, Nombre de Dios, VII-13-1954, Schilinger, 2 F (UCB); Nayarit State, 17 mi SE of Tepic, XII-18-1963, Toschi and Tauber, 14 M (UCB); Sonora State, Sr. delos Ajos, Pineoak, VI-1-1971, Roth, 50 MF (FAM). NEBRASKA: Dawes Co., Bordeaux Cr., V-31-1984, Lawson and Brown, 10 L (PERC); Chadron Cr., Chadron St. Pk., VI-16-1984, McCafferty and Provonsha, 10 L (PERC); same, pond at Chadron St. College, VI-15-1984, McCafferty and Provonsha, 4 M, (PERC); Sheridan Co., Beaver Cr., VI-22-1984, Brown, 5 L (PERC); Sioux Co., White Riv., IV-25-1978, Muenchau, 11 L (PERC); same, Sowbelly Cr., Sowbelly Cany., 8 mi N of harrison, VI-14-1984, McCafferty and Provonsha, 19 L (PERC). NEW MEXICO: Catron Co., Overflow pond, Scorpion Campground, Gila Nat'l Forest, V-6-1981, McCafferty, et al., 1 L (PERC); Grant Co., Cherry Cr., 2.4 mi N of Cherry Cr. Campground, VII-7-1964, Koss, et al., 1 M (PERC).

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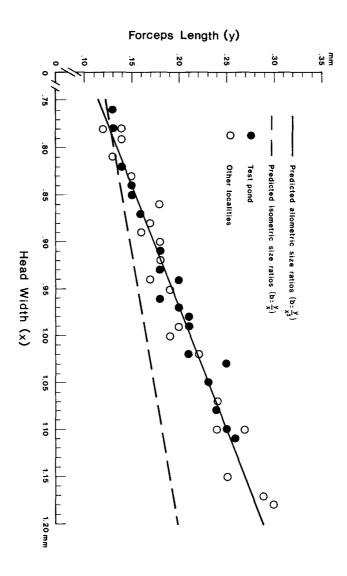


FIGURE 1. Allometry, C. latipennis male genital forceps length.

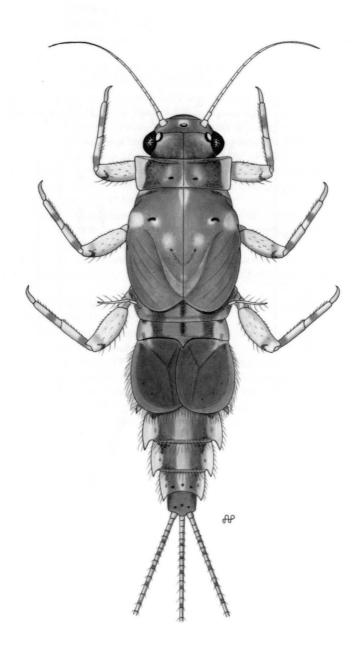


FIGURE 2. C. amica, larva, dorsal.

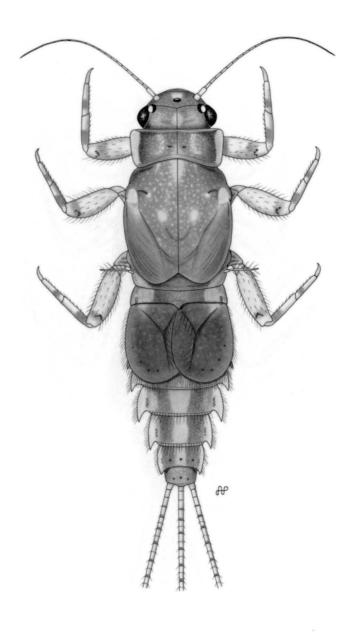


FIGURE 3. C. latipennis, larva, dorsal.

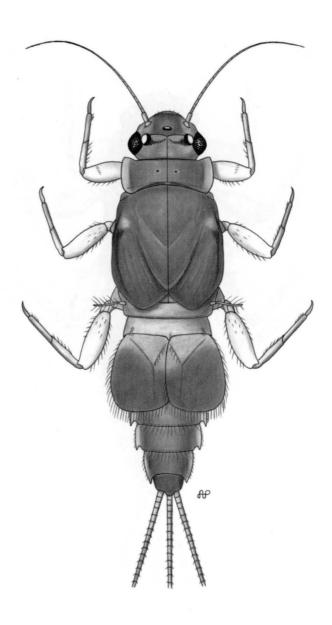


FIGURE 4. C. anceps, larva, dorsal.

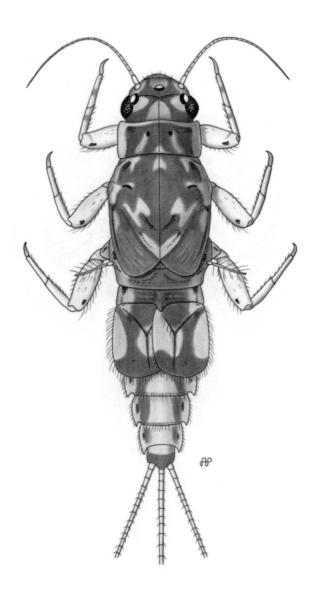


FIGURE 5. C. hilaris, larva, dorsal.

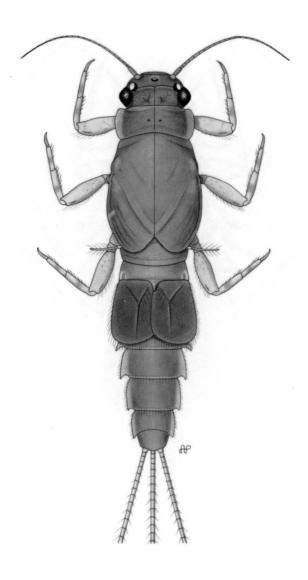


FIGURE 6. C. macafferti, larva, dorsal.

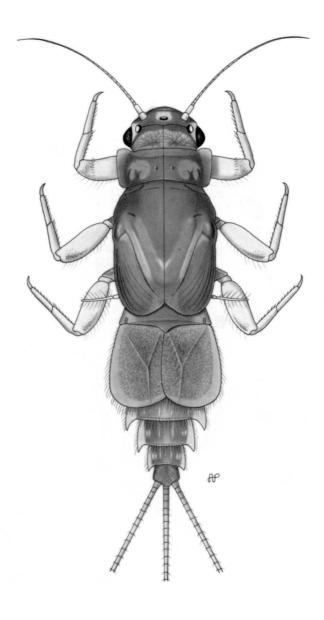


FIGURE 7. C. bajaensis, larva, dorsal.

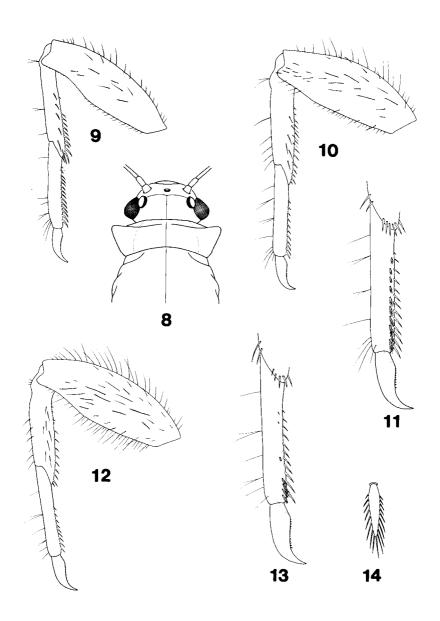
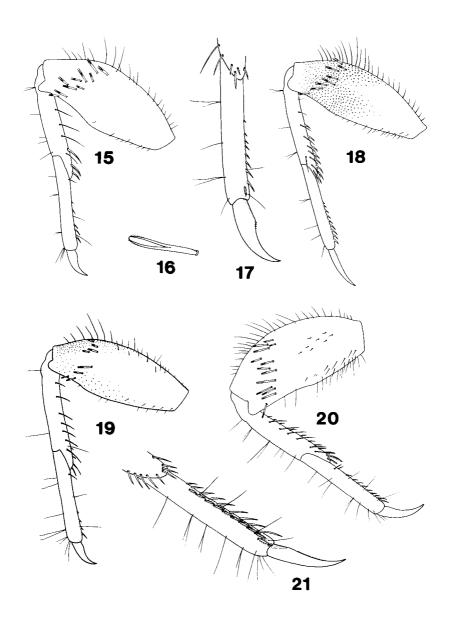
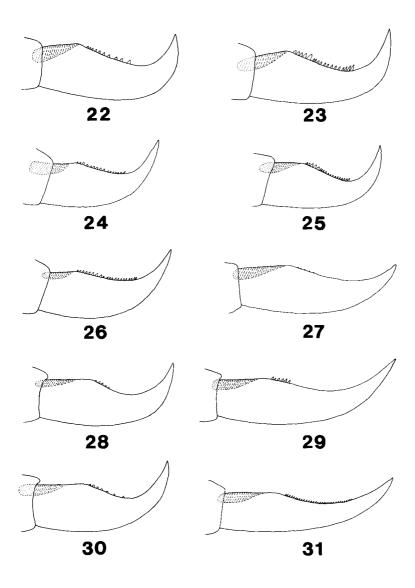


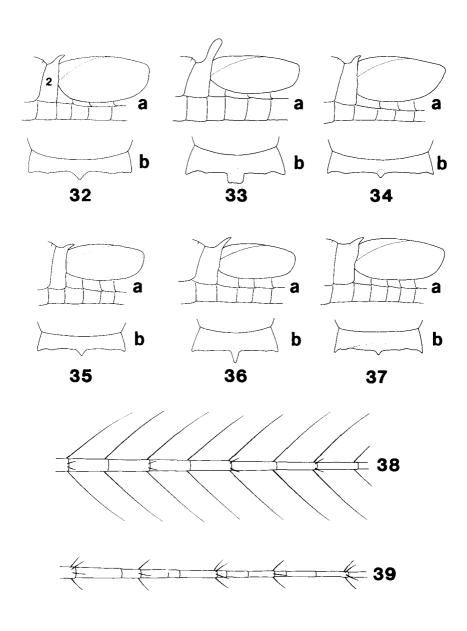
FIGURE 8-14. **8**, *C. youngi*, larval head and pronotum. **9-11**: *C. amica*, larva; **9**, foreleg, dorsal; **10**, hind leg, dorsal; **11**, hind tarsus, ventral. **12-13**: *C. latipennis*, larva; **12**, hind leg, dorsal; **13**, hind tarsus, ventral. **14**, fimbriate spur from venter of hind tarsus.



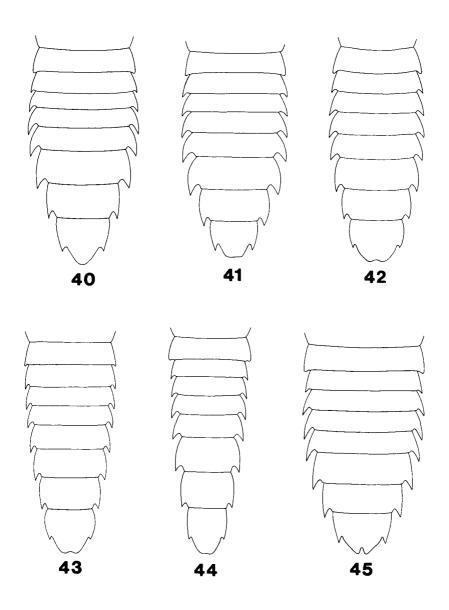
FIGURES 15-21. **15-17**: *C. hilaris*, larva; **15**, foreleg, dorsal; **16**, spatulate setae from forefemur; **17**, hind tarsus, ventral. **18**, *C. macafferti*, larval foreleg, dorsal. **19**, *C. anceps*, larval foreleg, dorsal. **20**, **21**: *C. bajaensis*, larva; **20**, foreleg, dorsal; **21**, hind tarsus, ventral.



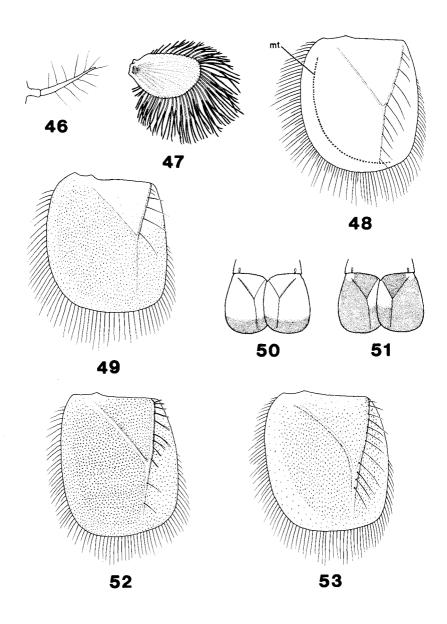
FIGURES 22-31. Hind tarsal claws; 22, C. amica; 23, C. diminuta; 24, C. latipennis; 25, C. punctata; 26, C. youngi; 27, C. anceps; 28, C. hilaris; 29, C. macafferti; 30, C. tardata; 31, C. bajaensis.



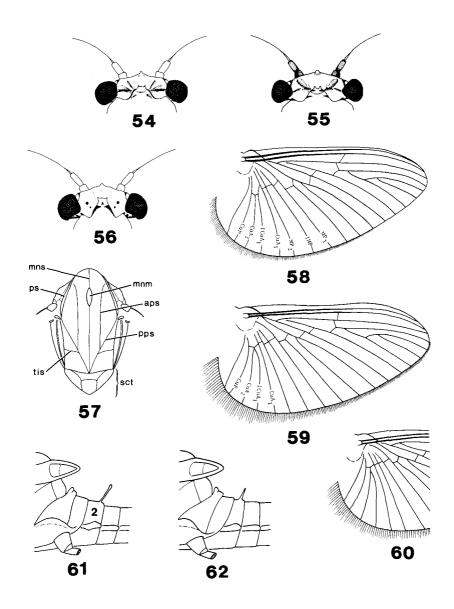
FIGURES 32-39. 32-37: Larval abdominal segment 2 (a-lateral, b-dorsal); 32, *C. amica*; 33, *C. youngi*; 34, *C. anceps*; 35, *C. hilaris*; 36, *C. macafferti*; 37, *C. bajaensis*. 38, 39: Caudal filaments, middle section; 38, *C. amica*; 39, *C. anceps*.



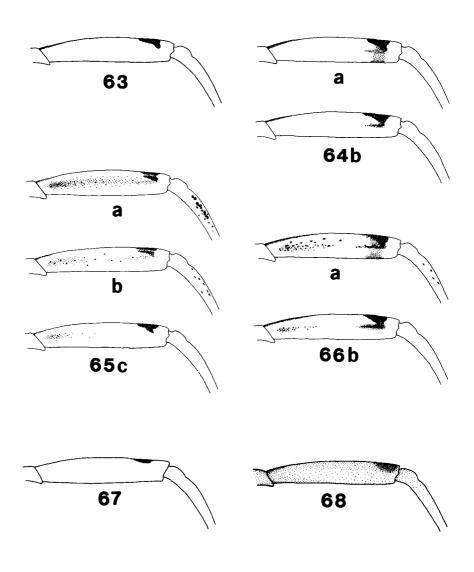
FIGURES 40-45. Larval abdomens, ventral; 40, C. amica; 41, C. latipennis; 42, C. anceps; 43, C. hilaris; 44, C. macafferti; 45, C. bajaensis.



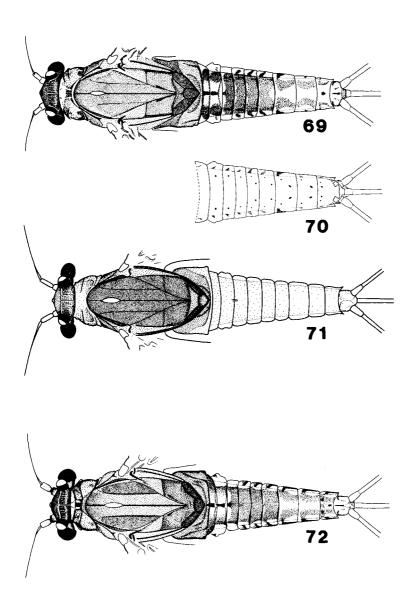
FIGURES 46-53. Larval gills; **46**, *Caenis* sp., gill 1; **47**, *Caenis* sp., gill 4; **48-53**: operculate gill 2; **48**, *C. amica*, mt = microtricial row on ventral surface); **49-51**: *C. hilaris*; **52**, *C. macafferti*; **53**, *C. tardata*.



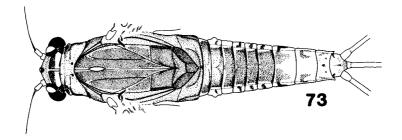
FIGURES 54-62. 54-56: Adult male head, ventral; 54, *C. amica*; 55, *C. diminuta*; 56, *C. latipennis*. 57, Adult mesothorax, dorsal; aps = anterior parapsidal suture, mnm = median notal membrane, mns = median notal suture, ps = prescutum, sct = scutellum, tis = transverse interscutal suture. 58-60: wings; 58, *C. amica*; 59, *C. hilaris*; 60, *C. bajaensis*. 61, 62: Adult, abdominal segment 2, lateral; 61, *C. youngi*; 62, *C. macafferti*.

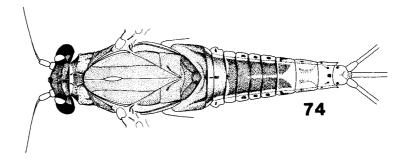


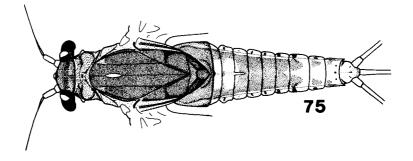
FIGURES 63-68. Adult hind femora; **63**, *C. amica*; **64** a, b, *C. diminuta*; **65** a-c, *C. latipennis*; **66** a, b, *C. punctata*; **67**, *C. hilaris*; **68**, *C. macafferti*.



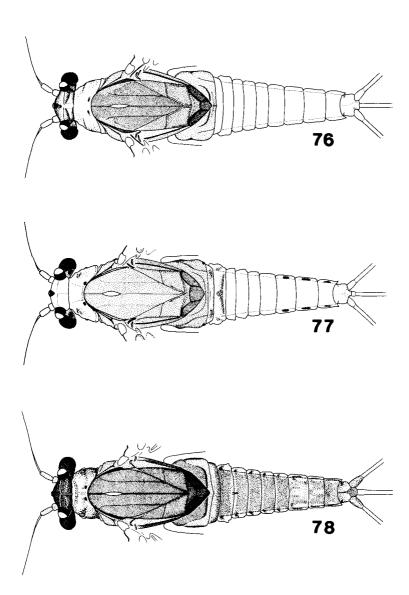
FIGURES 69-72. Adult male 69, C. amica; 70, C. amica, abdomen, ventral; 71, C. candida; 72, C. diminuta.



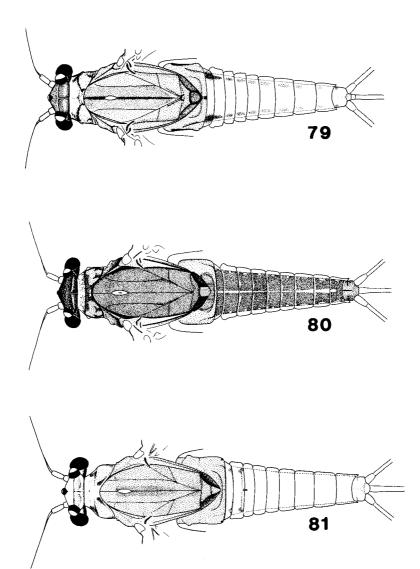




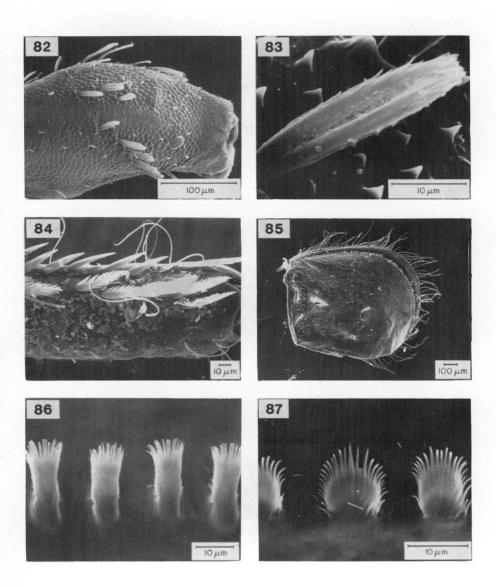
FIGURES 73-75. Adult male: 73, C. latipennis; 74, C. punctata; 75, C. youngi.



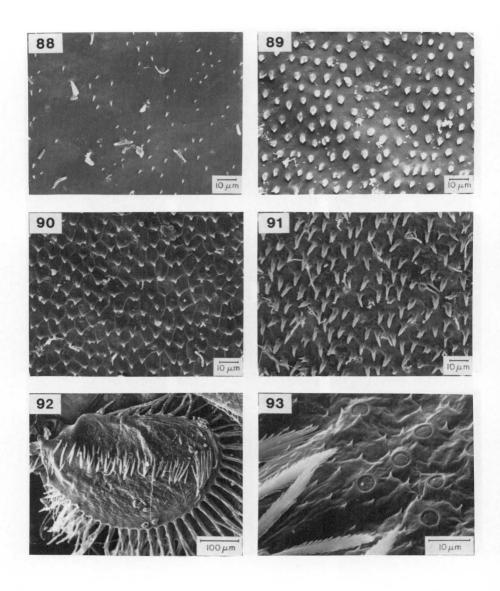
FIGURES 76-78. Adult male: **76**, *C. anceps*; **77**, *C. hilaris*; **78**, *C. macafferti*.



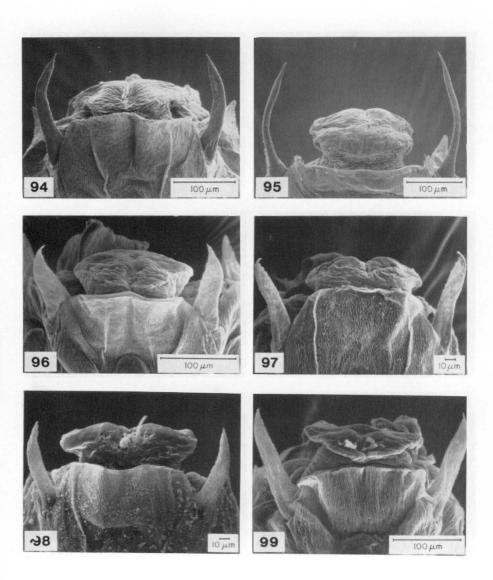
FIGURES 79-81. Adult male: 79, C. tardata; 80, C. bajaensis; 81, Amercaenis ridens.



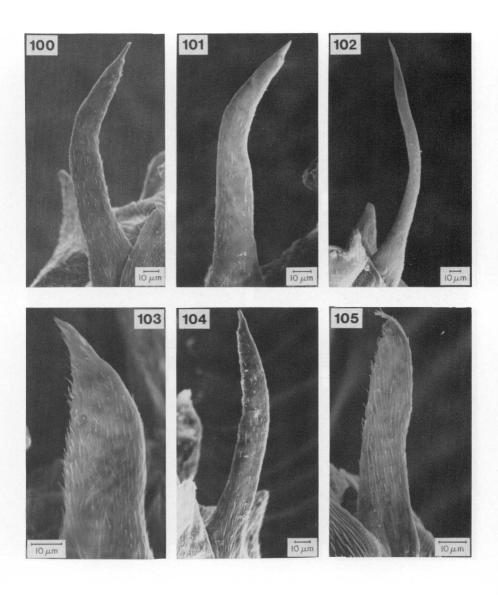
FIGURES 82-87. **82**, **83**; *C. hilaris*, larva; **82**, forefemur, dorsal; **83**, spatulate setae on forefemur. **84**, *C. bajaensis*. larval hind tarsus, ventral. **85**, *C. latipennis*, larval operculate gill, ventral. **86**, **87**: palmate setae [microtrichia] on ventur of operculate gill; **86**, *C. youngi*; **87**, *C. macafferti*.



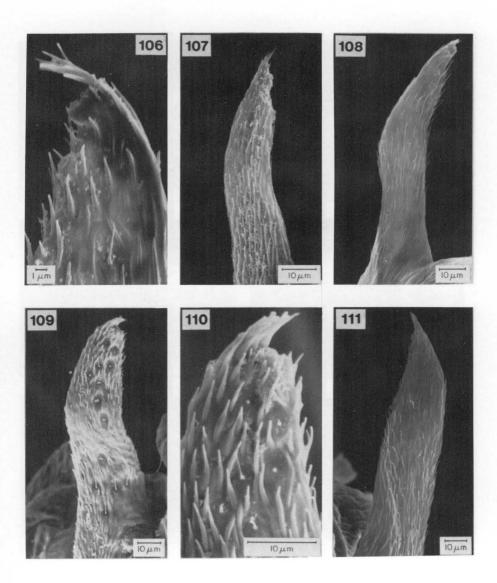
FIGURES 88-93. **88-91**: Operculate gill, dorsal surface; **88**, *C. amica*; **89**, *C. anceps*; **90**, *C. hilaris*; **91**, *C. macafferti*. **92**, *C. punctata*, gill 3, dorsal. **93**, *C. hilaris*, gill 3, dorsal surface.



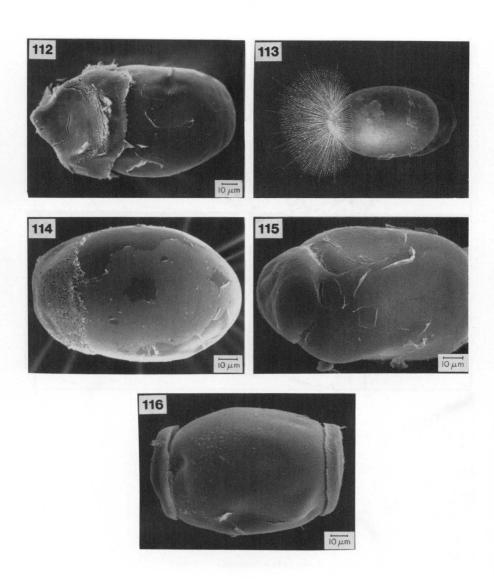
FIGURES 94-99. Male genitalia, ventral; 94, C. amica; 95, C. latipennis; 96, C. punctata; 97, C. anceps; 98, C. hilaris; 99, C. bajaensis.



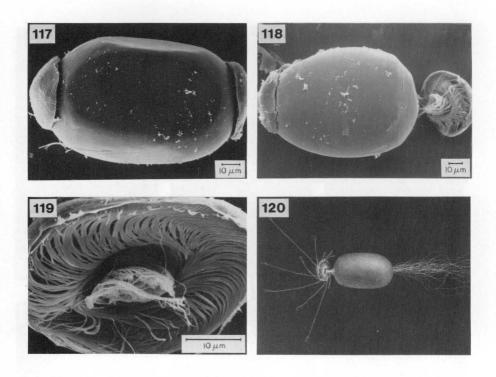
FIGURES 100-105. Male genital forceps, ventral; 100, C. amica; 101, C. diminuta; 102, C. latipennis; 103, C. punctata; 104, C. youngi; 105, C. anceps.



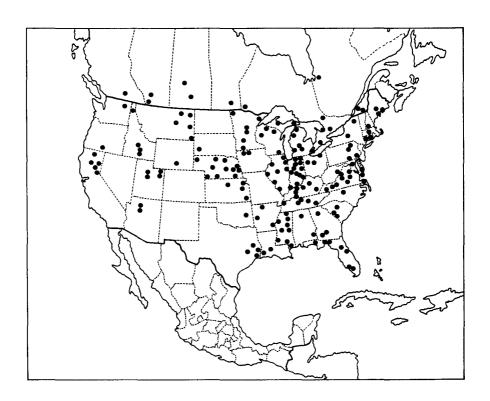
FIGURES 106-111. Male gennal forceps, ventral; **106**, *C. anceps*, forceps tip; **107**, *C. hilaris*; **108**, *C. macafferti*; **109**, *C. tardata*; **110**, *C. tardata*, forceps tip; **111**, *C. bajaensis*.



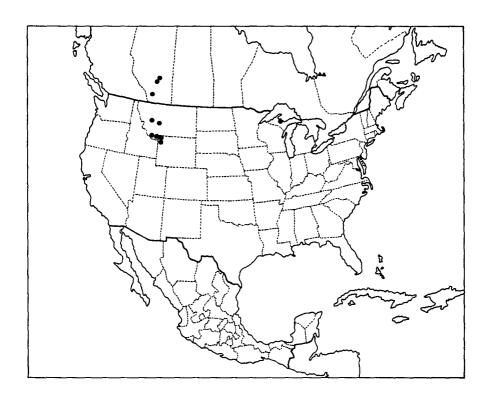
FIGURES 112-116. Eggs; 112, C. anceps; 113, C. anceps, attachment threads expanded; 114, C. hilaris; 115, C. macafferti; 116, C. bajaensis.



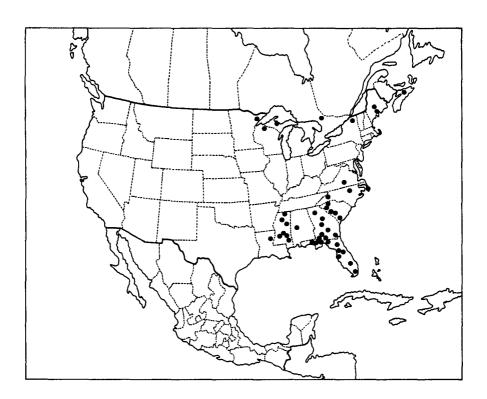
FIGURES 117-120. *C. latipennis* eggs; **117**, in dormant stage; **118**, with partially detached polar cap; **119**, inner view of polar cap; **120**, with attachment threads a = partially expanded; b = fully expanded).



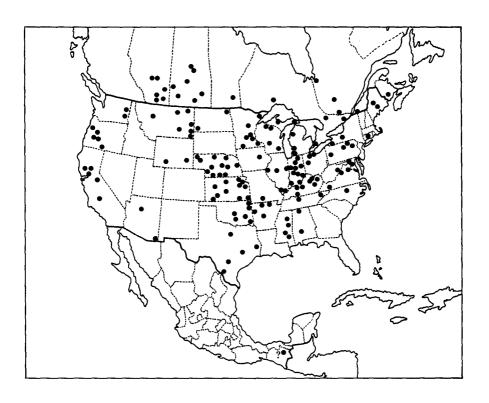
Map 1. Distribution of *C. amica*.



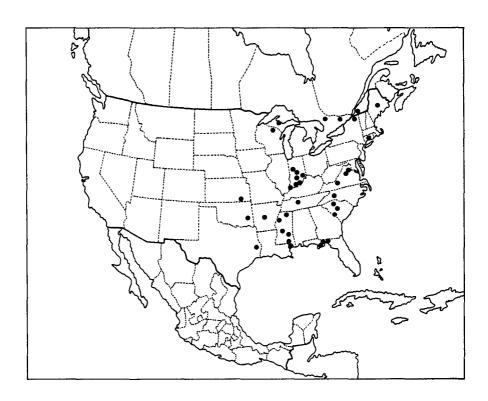
Map 2. Distribution of C. candida (triangles) and C. youngi (circles).



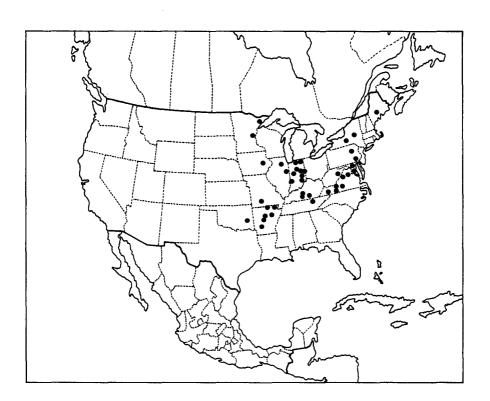
Map 3. Distribution of C. diminuta.



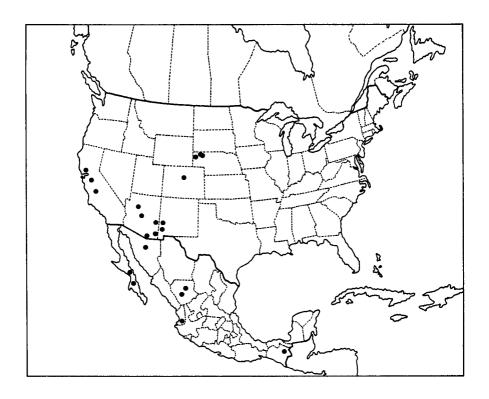
Map 4. Distribution of C. latipennis.



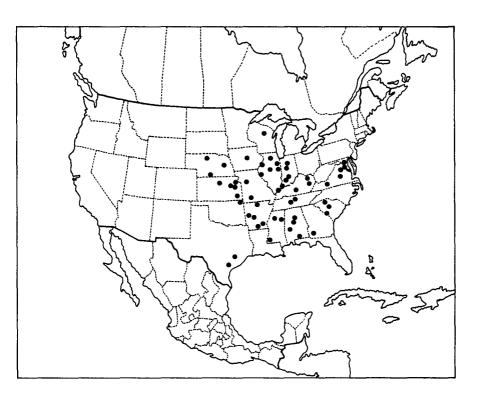
Map 5. Distribution of *C. punctata*.



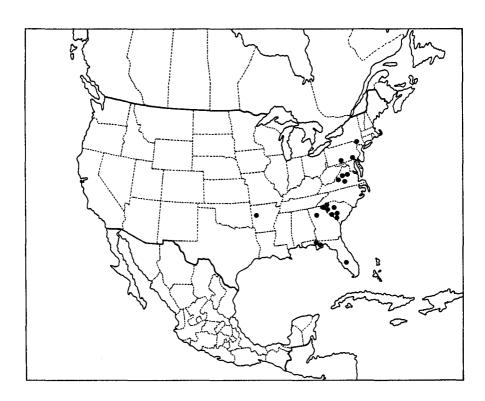
Map 6. Distribution of C. anceps.



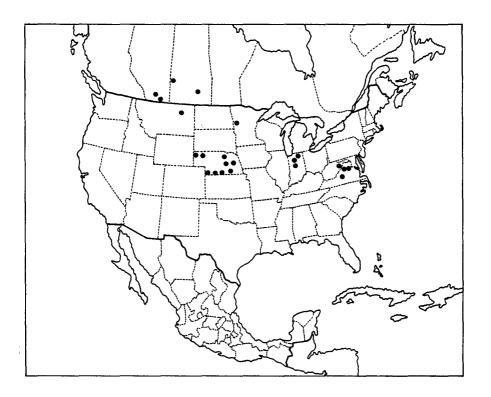
Map 7. Distribution of C. bajaensis.



Map 8. Distribution of C. hilaris.



Map 9. Distribution of C. macafferti.



Map 10. Distribution of C. tardata.