

Studies of Ephydrinae
(Diptera: Ephydriidae), V:
The Genera *Cirrula* Cresson
and *Dimecoenia* Cresson
in North America

WAYNE N. MATHIS
and
KARL W. SIMPSON

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of “diffusing knowledge” was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: “It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge.” This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 329

Studies of Ephydrinae
(Diptera: Ephydriidae), V:
The Genera *Cirrula* Cresson
and *Dimecoenia* Cresson
in North America

Wayne N. Mathis
and *Karl W. Simpson*



SMITHSONIAN INSTITUTION PRESS

City of Washington

1981

ABSTRACT

Mathis, Wayne N., and Karl W. Simpson. Studies of Ephydrinae (Diptera: Ephydridae), V: The Genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America. *Smithsonian Contributions to Zoology*, number 329, 51 pages, 119 figures, 1981.—The tribe Ephydrini is represented by four genera in North America: *Cirrula* Cresson, *Dimecoenia* Cresson, *Ephydra* Fallén, and *Setacera* Cresson. The adults are primarily surface skaters and have specially modified tarsi for this purpose. Most larvae have well-developed ventral prolegs and inhabit floating mats of filamentous algae. Diagnoses and generic keys are provided for the adults and third-instar larvae of North American Ephydrini.

Taxonomic and biological information is presented for the Nearctic species of *Cirrula* (*C. austrina* and *C. gigantea*) and *Dimecoenia* (*D. spinosa* and *D. fuscifemur*). For each species the adults, male and female, egg, three larval instars, and puparium (except for *D. fuscifemur*) are described and illustrated. Keys are provided for species identification of mature larvae and adults.

All four species occur only in coastal salt marsh habitats. The adults feed on microorganisms obtained from moist or wet substrates. Larvae of *Cirrula* inhabit mats of filamentous algae and closely resemble larvae of other Ephydrini (e.g. *Ephydra*) both structurally and biologically. Larvae of *Dimecoenia* inhabit mud substrates, and the mature larvae of one species, *D. spinosa*, tap the roots of aquatic macrophytic plants to obtain oxygen. The larval structure resembles that of more primitive Ephydridae, such as *Scatella* (Scatellini) and *Parydra* (Parydrinae).

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data

Mathis, Wayne N.

Studies of Ephydrinae (Diptera, Ephydridae)

Bibliography: p.

(Smithsonian contributions to zoology ; no. 285, 295, 303, 325, 329)

Includes bibliographies.

Contents: 1. Revisions of *Parascatella* Cresson and the trisetia group of *Scatella* Robineau-Desvoidy.—2. Mathis, W. N. Phylogeny, classification, and zoogeography of nearctic *Lamproscatella* Hendel.—[etc.]—5. Mathis, W. N., and Simpson, K. W. The genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America.

Supt. of Docs. no.: SI 1.27:329

1. Ephydridae—Classification. 2. Insects—Classification. I. Shewell, Guy E., joint author. II. Wirth, Willis Wagner, joint author. III. Simpson, Karl W., joint author. IV. Title. V. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 285 [etc.]

QL1.S54 no. 285, etc. [QL537.E7] 591s [595.77'4] 78-606062

Contents

	<i>Page</i>
Introduction	1
Acknowledgments	2
Methods	3
General	3
Collection and Rearing Techniques of Immatures	3
Preservation and Preparation of Immature Stages and Reared Adults	4
Measurements of Immature Structures and Presentation of Immature Descriptive Material	4
Abbreviations Used in Illustrations	5
Tribe EPHYDRINI Zetterstedt	5
Key to North American Genera and Subgenera of Ephydrini	7
Genus <i>Cirrula</i> Cresson	8
Key to Species of <i>Cirrula</i> Cresson	9
<i>Cirrula austrina</i> (Coquillett), new combination	9
<i>Cirrula gigantea</i> Cresson	21
Genus <i>Dimicoenia</i> Cresson	29
Key to Species of <i>Dimicoenia</i> Cresson	30
<i>Dimicoenia spinosa</i> (Loew)	30
<i>Dimicoenia fuscifemur</i> Steyskal	42
Literature Cited	49

Studies of Ephydrinae (Diptera: Ephydriidae), V: The Genera *Cirrula* Cresson and *Dimecoenia* Cresson in North America

Wayne N. Mathis
and Karl W. Simpson

Introduction

Shore flies, or members of the family Ephydriidae, comprise a diverse and remarkably versatile group of acalyptrate Diptera, with over 1200 species presently known. Their immature stages are mostly aquatic or semi-aquatic, and much of the interest in the family stems from their ability to breed in such seemingly adverse habitats as sulfurous hot springs, highly alkaline or saline water, or exposed pools of crude petroleum. This study concerns the genera *Cirrula* Cresson and *Dimecoenia* Cresson, the species of which occur in maritime salt marshes. These species, together with other members of the subfamily Ephydrinae that brook saline conditions, are commonly referred to as brine or salt flies.

As noted previously, *Cirrula* and *Dimecoenia* were proposed by Cresson in 1915 and 1916, respectively. Both genera occur only in North America.

Wayne N. Mathis, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560.
Karl W. Simpson, Division of Laboratories and Research, New York State Department of Health, Empire State Plaza, Albany, New York 12201.

The 13 Neotropical species assigned to *Dimecoenia* (Wirth, 1968) form a group that is morphologically distinct from the Nearctic species (Steyskal, 1970), and we agree with Wirth (1971) that they should be placed in a separate genus (a study of these species is in progress by the first author).

Since Cresson's initial proposal of *Cirrula* and *Dimecoenia*, there has been little mention of either genus in the literature except for occasional listings of species in faunistic studies of limited geographic coverage (Campbell and Denno, 1978; Johnson, 1913, 1925; Leonard, 1928). Sturtevant and Wheeler (1954) treated both genera in their synopsis of North American Ephydriidae, and Steyskal (1970) revised *Dimecoenia*. Steyskal (1970) demonstrated the usefulness of the male and female terminalia as diagnostic characters and figured these structures for *D. austrina* (Coquillett), *D. fuscifemur* Steyskal, and *D. spinosa* (Loew). Steyskal did not study *Cirrula gigantea* Cresson, but we have discovered that this species is very closely related to *D. austrina*. We are adjusting the classification to accommodate these discoveries (evidence and discussion to follow).

Even though *Cirrula* and *Dimecoenia* may be extremely abundant in tidal wetlands, they have not been subjected to intensive studies like many economically important Diptera because they do not interfere with human interests. Consequently, there is a paucity of information on the immature stages and natural history of both genera.

Previous work concerning the immature stages of Ephydrini includes the following:

Ephydra Fallén: Beyer (1939), Ping (1921), Simpson (1976, subgenera *Halephydra* Wirth and *Hydropyrus* Cresson), Trägårdh (1903), Wirth (1971, review), Zavattari (1921)
Ephydrella Tonnoir and Malloch: Dumbleton (1969)
 Neotropical "*Dimecoenia*": Hennig (1943), Oliveira (1954, 1958)
Setacera Cresson: Johannsen (1935)

Although natural history knowledge of the tribe is comparatively advanced, precise food sources for most species remained unknown until recently. By using a radioactive tracing technique, Brock et al. (1969) demonstrated conclusively that both larvae and adults of *Ephydra bruesi* feed on microorganisms, namely algae and bacteria occurring in algal mats of thermal spring effluents. In view of the biological and structural similarities between all members of the Ephydrini, the food resources utilized by these species are probably very similar (Simpson, 1979).

Among genera of the subfamily Ephydrinae, only *Cirrula* and *Dimecoenia* are exclusive inhabitants of maritime salt marshes, where their adults are frequently found to skate on the water's surface. Apparently their skating ability is directly related to structural features that partially characterize the tribe Ephydrini. All members of this tribe lack pulvilli and have moderately long tarsi. The lack of pulvilli precludes climbing on smooth surfaces, but the long tarsi, which are equipped ventrally with densely set hydrofuge hairs, enable adults to skate on the water's surface.

Larvae of *Cirrula* are typical of the tribe, having an elongate posterior respiratory tube, well-developed ventral prolegs, and patterns of dark markings dorsally (Figures 26, 27, 57, 58). They also inhabit the typical microhabitat for the tribe, namely mats of filamentous algae. Larvae of *Di-*

mecoenia are unlike any other known members of the tribe. They lack prolegs and dorsal markings and inhabit sand or mud substrates.

Two primary objectives are being served by this study. One is to clarify the systematics and phylogeny of *Cirrula* and *Dimecoenia* as part of ongoing research of the subfamily Ephydrinae by the first author. The second is to describe the immature stages and natural history of the included species, which is primarily the result of the second author's research. Although we have approached our research with different immediate objectives, we feel the division of labor has been beneficial and that the joint presentation of our studies here is complementary. Data from both studies were used in the formulation of conclusions and general observations.

ACKNOWLEDGMENTS.—Numerous individuals and institutions have contributed to this report. Without their cooperation and assistance, much of the study could not have been completed. We are grateful for their time and thoughtful consideration.

We thank the following curators and institutions for lending specimens (an asterisk indicates collections from which type-specimens were borrowed).

AMNH	American Museum of Natural History, New York; Dr. Pedro W. Wygodzinsky
ANSP*	Academy of Natural Sciences of Philadelphia; Dr. Daniel Otte
CAS	California Academy of Sciences, San Francisco; Dr. Paul H. Arnaud, Jr.
CNC	Canadian National Collection, Ottawa, Canada; Dr. J. R. Vockeroth
CU	Cornell University, Ithaca, New York; Dr. L. L. Pechuman
DLD	Personal collection of Dr. D. L. Deonier, Oxford, Ohio
KSU	Kent State University, Kent, Ohio; Dr. B. A. Foote
KU	University of Kansas, Lawrence; Dr. George W. Byers
MCZ*	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Ms. Margaret Thayer
NMW*	Naturhistorisches Museum, Wien, Austria; Dr. Ruth Lichtenberg

- OSU* Ohio State University, Columbus; Dr. Charles A. Triplehorn
 USNM* former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution

Ms. Holly B. Williams prepared all of the distribution maps and organized the locality data; Mr. L. Michael Druckenbrod and Ms. Elaine R. Hodges made most of the habitus illustrations; Victor Kranz prepared the wing photographs; Dr. Newton Perrins prepared the scanning electron micrographs; and Ms. Noreen Connell typed the final draft. An earlier draft was reviewed by Drs. C. O. Berg, B. A. Foote, and W. W. Wirth.

Methods

GENERAL.—We are generally following the procedures and descriptive format of adults as given in previous numbers of this series and elsewhere (Mathis, 1979a, 1979b, 1979c). Especially important is the definition of ratios and their formulations. One wing character needs further explanation.

Costagial Bristles: Basad of the costagial wing break (the break in the costa basad of the humeral break) are two large setae, for which we have adopted the term costagial bristles. One is inserted apically on the anterior surface, the other subapically on the dorsal surface. A comparison is made between the relative length of each.

Type-specimens of all nominal taxa have been studied. Label data accompanying each type are cited as given, with slashes to separate data of one label from another. Clarifying or interpretive comments are included in brackets. Abbreviations of institutions where specimens are deposited are those cited in the "Acknowledgments" section.

COLLECTION AND REARING TECHNIQUES OF IMMATURES.—One of the most successful methods for obtaining immature stages was to collect some of the suspected larval habitat in a plastic box and return it to the laboratory for processing. In the laboratory, the box was placed under fluores-

cent lighting and its contents were aerated, then checked periodically for larvae and puparia. Another method consisted of stirring up the substrate in situ and searching the water's surface for floating larvae and puparia that had become dislodged. Searching the undisturbed substrate was fruitful at times, but often proved to be very time consuming. A fourth method consisted of placing small portions of substrate in a vegetable strainer, thoroughly rinsing it, and searching the residue for immature stages.

Most of the rearings were made in the Freshwater Invertebrate Laboratory, Cornell University, where light was obtained from both natural sources and fluorescent fixtures. The temperature ranged between 19 and 26 degrees C. During extended field trips, rearing material was maintained in a vehicle in a manner similar to that in the laboratory.

In the laboratory, flies were anesthetized with carbon dioxide, determined to species, sexed, and placed in modified 40-dram plastic vials, which also served as adult breeding jars. Only one female was placed in each jar to assure that immature stages of only one species were obtained from each container.

The bottom substrate consisted of moist peat moss on which a portion of a salt marsh algal mat was placed to provide food and an oviposition site. A dab of honey and brewers' yeast paste was affixed to the jars, approximately 1.0 cm from the bottom, as a diet supplement. Maintenance of rearing containers in a condition under which flies could survive was a major problem. Although the jars were supplied with fresh algae daily, many flies died with extremely flattened abdomens, suggesting that they had starved. Their nearly constant grazing of the algae rapidly depleted the food supply, and their frequent defecation quickly fouled the containers. Consequently, the longevity and oviposition values reported here from laboratory-maintained flies may be substantially lower than those occurring in nature.

Eggs were removed from the jars and transferred to small plastic rearing boxes by a moist-

ened camel's hair brush. Each box was fitted with two layers of moist paper toweling, on which the eggs were placed. Larvae usually were segregated into individual rearing boxes after hatching to insure accurate determination of individual stadial lengths. Larvae were checked daily for development and provided with fresh food (portions of field-collected salt marsh algal mats). After puparia were formed, they were transferred to moist cotton at the bottom of 4-dram vials. The vials were then plugged with cotton and checked daily for newly emerged adults.

PRESERVATION AND PREPARATION OF IMMATURE STAGES AND REARED ADULTS.—Eggs were placed directly into KAAD. Larvae were killed and fixed in water heated to just below the boiling point, then preserved in 70% ethanol. Puparia were lanced several times with a number one insect pin and placed in 70% ethanol. Cast exuviae of first- and second-instar larvae were found by carefully checking the larval rearing dishes after a molt had occurred. These exuviae were placed on microscope slides in a small drop of glycerine, and later provided material for describing and illustrating structures of the first- and second-instar larvae. Structures of third-instar larvae were obtained by placing freshly killed larvae in tap water and letting them decompose. After a few days, the sclerotized structures were easily separated from the soft parts of the larvae, which had become flaccid. The sclerotized structures were then placed in glycerine on microscope slides.

Newly emerged adults not used for rearing purposes were killed two to four days after emergence, thus allowing sufficient time for the exoskeleton to become fairly rigid. Puparia which had produced imagines were placed in number four or five gelatin capsules and pinned beneath their respective adults. Parasitoid wasps were placed on cardboard points above the puparia from which they emerged.

MEASUREMENTS OF IMMATURE STRUCTURES AND PRESENTATION OF IMMATURE DESCRIPTIVE MATERIAL.—Measurements were made with ocular micrometers that had been calibrated.

Terminology for the larval structures usually follows that used by Eastin and Foote (1971), Foote and Eastin (1974), and Busacca and Foote (1978). The term "interspiracular process" has been replaced with "hydrofuge lamella," because of this feature's function (flotation) and structure as shown by scanning electron microscopy (Figure 35). In addition, these structures are not located between the spiracular openings as they are in most dipterous larvae, so the term "interspiracular" is misleading. The paired posterior spiracular discs, typical of many cyclorrhaphous larvae, form a terminal cap on each branch of the respiratory tube, and hence are termed "posterior respiratory caps." "Lateral pharyngeal process" has been coined for the round sclerite in the anterior sinus on each side of the pharyngeal sclerite. The "indentation index" of the pharyngeal sclerite is the length of the sinus separating the dorsal and ventral cornua/total length of the pharyngeal sclerite $\times 100$. Two distances were measured to estimate body length, since the angling of the posterior respiratory tube makes a single linear measurement difficult. "Main body length" is the distance from the anterior end of the specimen to the posterior margin of its anal proleg. "Respiratory tube length" is the distance from the posterior base of the anal proleg to the apex of the *fully extended* respiratory tube. This structure is partially retracted in many preserved specimens, but is easily extended to its full length by grasping the apex with a pair of fine forceps and gently pulling posteriorly while holding the body of the larva.

Segments one and two are also variously retracted in preserved specimens, but no method was discovered to standardize their position. An attempt has been made to illustrate and describe these segments either fully evaginated or invaginated, but this has not always been possible.

Mean values are given for the sizes of all eggs and puparia in addition to the range of values. These two stages have a fixed structure, and the mean value for each, therefore, gives an indication of the size of the average specimen. Only the ranges are given for each larval instar because the

size of the larva depends on its age and on the suitability of its habitat. The overlap between successive instars, usually indicated in these ranges, reflects the fact that well-grown and extended individuals before a molt are often larger than siblings that are preserved just after that molt. Size ranges for larvae of successive instars that do not overlap probably reflect a lack of sufficient material to represent the entire range of larvae within one or both instars.

To standardize variations of certain sclerotized structures, fully grown larvae of all three instars were used for the descriptions. For example, the dorsal patterns and spines on the larvae are darker on fully grown third-instar larvae than on newly molted larvae of the same instar. Also, the posterior spiracular caps of some species increase in length basally as the larvae of each instar develop.

ABBREVIATIONS USED IN ILLUSTRATIONS.—Several of the illustrations, especially those of *C. austrina*, have various structures that have been labeled with the following abbreviations:

A	antenna
ABH	anterior hypostomal bridge
ASp	anterior spiracle
CSP	circular sensory plate
DB	dorsal bridge
DC	dorsal cornua
DS	dentate sclerite
ES	epistomal sclerite
HL	hydrofuge lamella
HS	hypostomal sclerite
ILR	inner longitudinal rod
LPP	lateral pharyngeal process
LR	longitudinal rod
LS	ligulate sclerite
M	micropyle
MBL	main body length
MH	mouthhook
OLR	outer longitudinal rod
OS	oral spinule
PB	parastomal bar
PHB	posterior hypostomal bridge
PRT	posterior respiratory tube
PoSB	postoral spine band
PS	pharyngeal sclerite
PSC	posterior spiracular cap

RTL	respiratory tube length
S	sensillum
SpO	spiracular opening
SpS	spiracular scar
TSP	transverse sclerotized plate
VC	ventral cornua
W	window

Tribe EPHYDRINI Zetterstedt

EPHYDRINI Zetterstedt, 1837:48 [as the "family" Ephydri-
nae].—Wirth and Stone, 1956:46 [first use formally as a
tribe].

DIAGNOSIS.—Specimens of Ephydrini may be distinguished from other Ephydridae by the following combination of character states.

Adults: Mesofrons subquadrate, becoming slightly wider posteriorly, with shiny, metallic luster; frequently with convergent intrafrontal bristles inserted near anterior margin of mesofrons; dorsum of interfoveal carina usually shiny, concolorous with mesofrons; facial setae along oral margin usually dense and long; dorsocentral bristles 5 pairs, sometimes anterior pairs weak; intrapostalar bristle well developed, at least equal to one-half length of postalar bristle; supra-alar bristle well developed, subequal to postalar bristle; propleuron setulose; prosternum setose, usually more evident along posterior margin near front coxae; hind coxal strap setose; pulvilli rudimentary or lacking; tarsal claws shallowly curved and usually elongate.

Third-Instar Larva: Mouthhooks not joined together basally, each mouthhook spatulate and dentate marginally; anterior spiracles present, with 2–8 marginal papillae; posterior spiracles borne distally on a bifid, retractile respiratory tube, tube one-third to one-sixth total body length; spiracular caps each bearing 4 spiracular openings (or series of openings), openings slitlike and each bordered basally by a hydrofuge lamella; segments 5–12 with ventral prolegs bearing crochetlike spines in well-defined rows; dorsal patterns composed of flattened spines usually present; if prolegs and dorsal patterns absent,

then spiracular openings subdivided and spiracular caps elongate.

DISCUSSION.—Larvae of most Ephydrini are easily recognized by their elongate respiratory tube, ventral prolegs, and dorsal spine patterns. Larvae of *Dimiscoenia* lack the last two characters and superficially resemble those of some other mud-inhabiting Diptera, including among the Ephydriidae the following: *Parydra* (Deonier and Regensburg, 1978), *Paracoenia* (Beyer, 1939), and *Ochthera* (Simpson, 1975). The larvae of *Dimiscoenia* should be distinguishable on the basis of their mouthparts, the unique structure of the posterior spiracles, and their habitat distribution (salt marshes).

The monotypy of this tribe is well established, being based on the following autapotypies:

1. Setal vestiture of prosternum: in members of this tribe, the prosternum is setose, especially ventrally and posteriorly around the coxal cavities and usually more extensively. The generalized condition in the family is for the prosternum to be bare of setae.

2. Hind coxal strap: the hind coxa has a strap that extends around the posterior side. This strap bears four or five setae in members of Ephydrini. Elsewhere in the family it is bare.

3. Pulvilli: with few exceptions in the family, the pulvilli are evident as conspicuous pads beneath the tarsal claws. In members of Ephydrini, however, the pulvilli are either rudimentary or are lacking entirely.

4. Tarsal claws: the tarsal claws are shallowly curved and are usually elongate in members of Ephydrini. The generalized condition is for claws to be conspicuously curved and short.

5. Larval prolegs: with the exception of a secondary reversal in *Dimiscoenia*, larvae of Ephydrini have prominent, ventral prolegs that bear crochets. These structures are an adaptation to the typical algal-mat habitat of the immatures of these flies and assist in grasping the substrate. The secondary reversal in larvae of *Dimiscoenia* apparently occurred as the latter shifted back to

a mud-shoreline habitat. Larvae of *Dimiscoenia* have small creeping welts, similar to those of other mud-inhabiting Ephydriidae.

6. Habitat of immatures: the generalized habitat for the subfamily Ephydrinae is shoreline mud. This is the habitat of most species of Scatellini and of several genera of the subfamily Parydrinae. Members of Ephydrini, however, have adapted to algal mats on the surface of both lentic and lotic water systems.

Ephydrini is one of several monophyletic lineages arising from the ancestral lineage that now comprises the concept of Scatellini (Mathis, 1979c, 1980). The actual sister-group of Ephydrini probably gave rise to the *Paracoenia-Calocoenia* group of genera. This latter lineage plus Ephydrini, as here delimited, is characterized by the following character states (some have become modified secondarily):

1. Number of dorsocentral bristles: although other genera of the subfamily Ephydrinae sometimes have five pairs of dorsocentral bristles (e.g. *Notiocoenia* Mathis and *Austrocoenia* Wirth), the anterior pair (or pairs) is weakly developed. Only in members of the lineage *Paracoenia-Calocoenia* plus Ephydrini are there five well-developed pairs (the anterior pair is presutural; specimens of *Cirrula gigantea* have the anterior four pairs of dorsocentral bristles weakly developed, a condition we interpret to be secondary).

2. Development of intrapostalar bristle: in most species of the family, the intrapostalar bristle is either lacking or is very much reduced, less than one-half the length of the postalar bristle. In members of this lineage, the intrapostalar bristle is frequently as long as the postalar bristle.

3. Setal vestiture of propleuron: throughout most of the family this pleural sclerite is bare of setae (although frequently it is pollinose to densely tomentose). In members of this lineage, there are numerous setulae that are generally conspicuously evident.

A more detailed account of the tribes and genera of Ephydrinae will be forthcoming in a generic revision that is now in progress.

Key to North American Genera and Subgenera of Ephydrini

ADULTS

1. Third antennal segment with a large bristle inserted laterally just below insertion of arista **Setacera** Cresson
 Third antennal segment lacking a large bristle 2
2. Posthumeral bristle present, subequal to size of posterior notopleural bristle; 3-4 pairs of laterocline fronto-orbital bristles (genus *Ephydra* Fallén) 3
 Posthumeral bristle either lacking or much reduced, not distinguishable from surrounding setulae; 2 pairs of laterocline fronto-orbital bristles 5
3. Two pairs of presutural dorsocentral bristles; bristles along oral margin elongate, subequal to height of eye; arista with basal one-third abruptly swollen, apical two-thirds stylelike; cruciate intrafrontal bristles usually 2 pairs; front basitarsus of male with a ventral tuft of long hairs near apex Subgenus **Hydropyrus** Cresson
 One pair of presutural dorsocentral bristles; bristles along oral margin not more than one-half eye height; arista thickened basally but gradually tapering to stylelike apex; cruciate intrafrontal bristles either lacking or with 1 pair; front basitarsus of male lacking ventral tuft of hairs 4
4. Cruciate intrafrontal bristles well developed, 1 pair; posterior crossvein making nearly right angle at merger with vein CuA₁; mesonotum shiny to moderately sparsely cinereous Subgenus **Ephydra** Fallén
 Cruciate intrafrontal bristles lacking or weakly developed; posterior crossvein making an acute angle at merger with vein CuA₁; mesonotum densely whitish cinereous Subgenus **Halephydra** Wirth
5. Arisal rays short, length approximately one-half width of second antennal segment; dorsal costagial bristle nearly twice length of anterodorsal costagial bristle; hind femur of male conspicuously turgid, with short row of 4-5 stout setae along anteroventral surface toward base; hind tibiae of male with ventroapical tuft of hairs; hind tarsi of male variously modified **Cirrula** Cresson
 Arisal rays long, length subequal to width of second antennal segment; dorsal costagial bristle subequal to length of anterodorsal costagial bristle; hind femur of male not differing markedly from middle or front femur, lacking stout setae as above; hind tibiae of male lacking tuft of hairs; hind tarsi of male normal, cylindrical **Dimcoenia** Cresson

THIRD-INSTAR LARVAE

1. Ventral prolegs well developed 2
 Ventral prolegs inconspicuous or lacking **Dimcoenia** Cresson
2. Venter of segment 3 with transverse sclerotized strap 3
 Venter of segment 3 without a continuous sclerotized process 4
3. Sclerotized strap of segment 3 about 3 times as wide as long, its margin

- broadly and irregularly sinuate; inhabitants of inland mineral waters *Ephydra*, Subgenus *Hydropyrus* Cresson
- Sclerotized strap 6–10 times as wide as long, its margin straight; inhabitants of maritime salt marshes *Cirrula* Cresson
4. Posterior respiratory tube with a pair of accessory filaments (tubules) near its base *Ephydra*, Subgenus *Halephydra* Wirth
- Posterior respiratory tube without filaments, but may have tubercles that are no longer than wide 5
5. Dorsal patterns of flattened spines present; inhabitants of saline, alkaline, and/or thermal waters *Ephydra*, Subgenus *Ephydra* Fallén
- Dorsum with numerous spines and spinules, but none are flattened to form distinct dorsal patterns; inhabitants of fresh waters .. *Setacera* Cresson

Genus *Cirrula* Cresson

Cirrula Cresson, 1915:70 [type-species: *Cirrula gigantea* Cresson, by monotypy].—Sturtevant and Wheeler, 1954:162–163 [review].—Wirth, 1965:753 [catalog].

Pogonephydra Hendel, 1917:42 [type-species: *Pogonephydra chalybea* Hendel (= *C. gigantea*), by monotypy]. [Synonymy by Hendel, 1931:10.]

DIAGNOSIS.—Specimens of *Cirrula* may be distinguished from those of other genera of the tribe by the following combination of character states.

Adults: Cruciate intrafrontal bristles 1 pair, sometimes reduced; laterocline fronto-orbital bristles 2 pairs, slightly divergent; third antennal segment simple, lacking secondary bristle inserted laterally just below arista; arista bare apically, basal aristal rays short, length no longer than approximately one-half width of second antennal segment; posthumeral bristle lacking; prescutellar bristles lacking; dorsal costagial bristle of wing nearly twice length of anteroventral costagial bristle; costa with numerous, generally evident, spinelike setae, but not as large as in *Dimecoenia*; hind femur of male turgid (best seen by comparing with femora of middle and front legs), bearing row of stout setae along anteroventral surface; hind tibiae of male with ventroapical tuft of long hairs; hind tarsi of male variously modified; aedeagus bifurcate, posterior lobe enlarged apically to form more or less rectangular process, anterior lobe variously shaped; female receptacle with

large operculum, generally as long as wide, extending process J-shaped, length about as long as operculum.

Third-Instar Larva: Ventral prolegs 8, well developed, each bearing distinct rows of crochetlike spines; third segment with transverse sclerotized strap ventrally; larvae inhabitants of filamentous algal mats in maritime salt marshes.

DISCUSSION.—We have enlarged the concept of *Cirrula* to accommodate *C. austrina*, the sister species of *C. gigantea*. These two species together form a monophyletic group that is characterized by the following autapotypies:

1. Legs: several characters of the legs are sexually dimorphic. The following characters are modified in males: Femur of hind leg conspicuously turgid (best seen by comparing with femur of middle leg); tibia of hind leg with ventroapical patch of long hairs (this character state also appears, by convergence, in some specimens of *Setacera*); tarsi of hind leg variously modified, usually explanate to some degree and bearing longer setae, especially basal tarsomere.

2. Venter of third segment of third-instar larva: on the venter of the third segment both species have a sclerotized straplike transverse band that is usually dark colored. Larvae of *Ephydra hians* Say have a similar band, although it is much longer and more irregular in shape (Simpson, 1976), thus indicating a close relationship between *Cirrula* and *Ephydra hians*.

Key to Species of *Cirrula* Cresson

ADULTS

Anterior 4 pairs of dorsocentral bristles, presutural bristles, and cruciate intrafrontal bristles weak, barely discernable from surrounding setulae; face with dense patch of long bristles subdorsally; parafrons blackish brown, appearing velvety; front tarsi of male broadly explanate laterally

Cirrula gigantea Cresson

Five pairs of dorsocentral bristles, presutural bristle and cruciate intrafrontal bristles well developed, conspicuously larger than surrounding setulae; face lacking dense patch of long bristles subdorsally; parafrons brownish, appearing pollinose; front tarsi of male cylindrical, similar to tarsi of middle leg

Cirrula austrina (Coquillett)

THIRD-INSTAR LARVAE

Transverse sclerotized strap on venter of third segment with posterior projection, although lighter colored (Figure 49); overall length up to 17.5 mm; cephalopharyngeal skeleton length 0.9–1.0 mm .

Cirrula gigantea Cresson

Transverse sclerotized strap on venter of third segment lacking posterior projection (Figure 13); overall length up to 14 mm; cephalopharyngeal skeleton length 0.7–0.8 mm

Cirrula austrina (Coquillett)

Cirrula austrina (Coquillett), new combination

FIGURES 1–36, 111, 115, 116

Ephydra austrina Coquillett, 1900:36.—Aldrich, 1905:629 [catalog].

Caenia [sic] *virida* Hine, 1904:65 [description].—Cresson, 1916:152 [synonymy].

Ephydra viridis.—Aldrich, 1912:100 [review].

Dimecoenia austrina.—Cresson, 1916:152 [diagnosis].—Sturtevant and Wheeler, 1954:166 [review].—Wirth and Stone, 1956:472 [review].—Wirth, 1965:755 [catalog].—Steyskal, 1970:463 [review, figures of male and female terminalia].

DIAGNOSIS.—Specimens of *C. austrina* may be distinguished from those of *C. gigantea* by the following combination of character states.

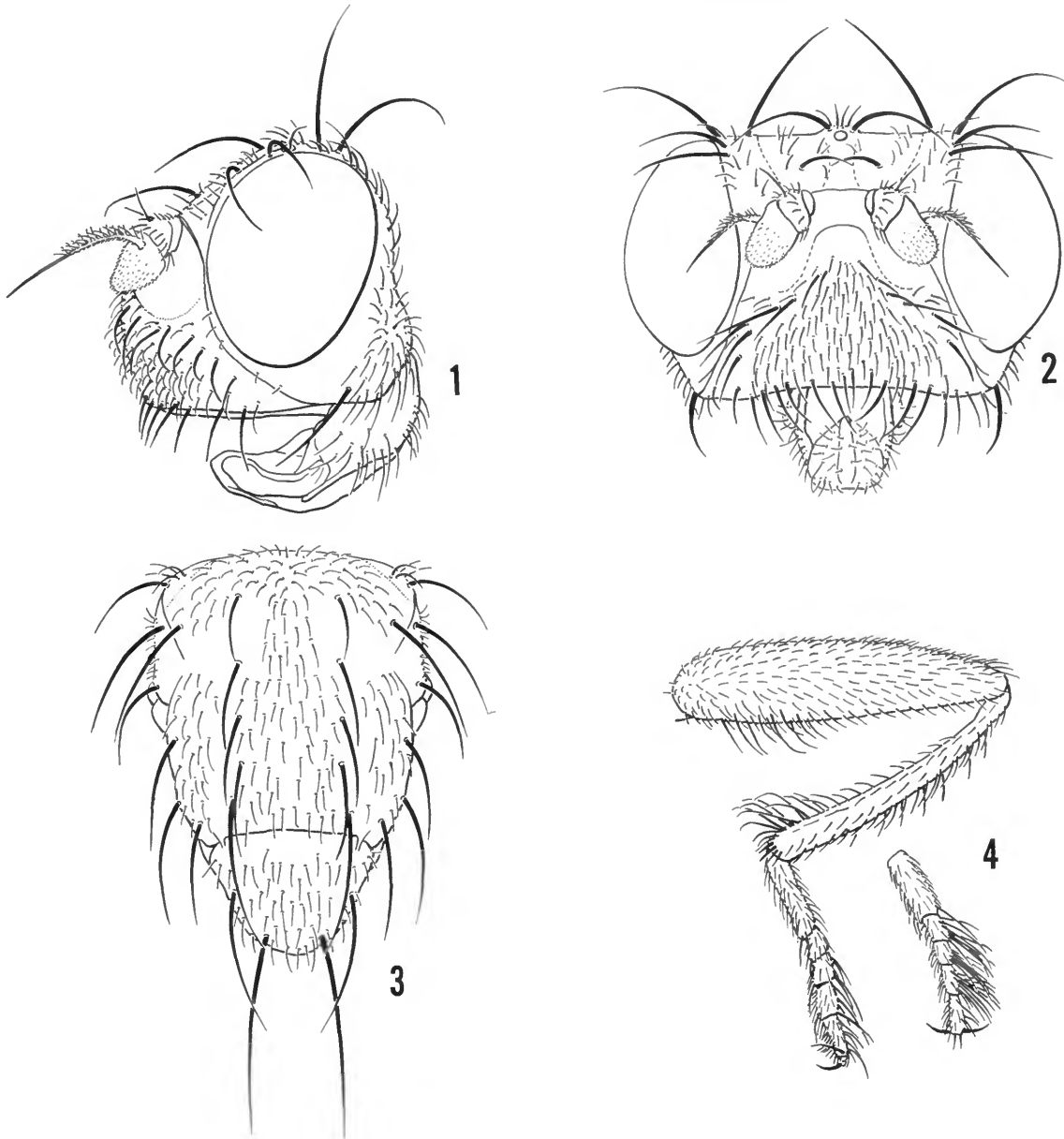
Adults: Laterocline fronto-orbital bristles large; cruciate intrafrontal bristles large, over two-thirds length of arista, overlapping apically; parafrons brownish to brownish gray, pollinose but not velvety; aristal rays slightly longer than aristal width at base; face lacking dense patch of long bristles subdorsally; dorsocentral bristles 5 pairs, well developed, all subequal; presutural bristles well developed, equal to or longer than anterior notopleural bristle; tarsi of front leg nor-

mal, cylindrical, similar to those of middle leg; hypandrium evident as well-sclerotized process; setae of epandrium around cercal cavity similar to other epandrial setae.

Third-Instar Larva: Transverse sclerotized strap of third segment approximately 10 times as wide as long and lacking posterior projection; overall length up to 14 mm; cephalopharyngeal skeleton 0.7–0.8 mm in length.

DESCRIPTION OF ADULT.—Moderately large to large shore flies, length 4.83 to 6.81 mm; mostly dull, olivaceous to grayish brown with subshiny to shiny areas on dorsum.

Head (Figures 1, 2): Head width-to-height ratio averaging 1 : 0.58; frons width-to-length ratio averaging 1 : 0.51, mesofrons with median shallow depression between median ocellus and ptilinal suture, shiny, with metallic olivaceous to greenish blue luster; cruciate intrafrontal bristles 1 pair, large, overlapping apically; remainder of mesofrons with small, generally inconspicuous setulae; ocellar triangle and parafrons mostly colorous, brownish to brownish gray, parafrons



FIGURES 1-4.—*Cirrula austrina*: 1, head, lateral aspect; 2, head, anterior aspect; 3, thorax, dorsal aspect; 4, hind leg of male, lateral aspect and dorsal aspect of tarsi.

becoming slightly darker anteriorly; ocelli arranged to form equilateral or isosceles triangle, if latter posterior ocelli closer to each other than to median ocellus; lateroclinate fronto-orbital bris-

cles large; postocellar setae only moderately well developed; postocular setae more or less uniform in size. Antenna mostly unicolorous, brownish gray to charcoal gray; arista longer than com-

bined length of first 3 antennal segments, tapering gradually from thickened base to stylelike apex; subpectinate dorsally from base to just apical of midpoint, rays less than one-half width of second antennal segment. Face width-to-height ratio averaging 1 : 0.73, interfoveal carina prominent, dorsum shiny, nearly concolorous with shiny mesofrons; antennal fovea deeply depressed, ventral margin sloping ventrally at conspicuous angle, more or less concolorous with remainder of face but less pollinose and tending to be somewhat subshiny with very light greenish blue reflections; face olivaceous to argenteous, darker dorsally; marginal facial setae larger, extending from interfoveal carina to posteroventral corner of face more or less uniformly, gently curved, posterocline; oral margin shallowly emarginate toward middle. Eye width-to-height ratio averaging 1 : 1.2, eye-to-cheek ratio averaging 1 : 0.29; gena moderately wide, mostly bare except for small setae paralleling parafacial suture, mostly concolorous with face, becoming darker and setulose posteriorly.

Thorax (Figure 3): Mesonotum generally subshiny, slightly darker and shinier posteriorly, with longitudinal pollinose vittae between shiny ones, particularly evident anteriorly, color varying from grayish blue to metallic olivaceous green; acrostichal setae uniseriate; dorsocentral bristles 5 pairs, all subequal in size, well developed. Pleural areas lighter and more pollinose than mesonotum, becoming lighter and grayer toward venter. Legs generally dark colored, dull, pollinose, unicolorous for the most part, apices generally tawny; legs of male differing as follows: hind femur (Figure 4) enlarged, swollen, particularly basal half, with row of stout setae along anteroventral surface; hind tibia (Figure 4) with several long hairs on ventral surface near apex; hind tarsomeres generally shorter, slightly more swollen, bearing tufts of long hairs on ventral surfaces, more pronounced on basal tarsomeres. Wing (Figure 11) length averaging 4.76 mm; generally hyaline, or but slightly infumated, grayish brown; costal vein index averaging 1 : 0.19;

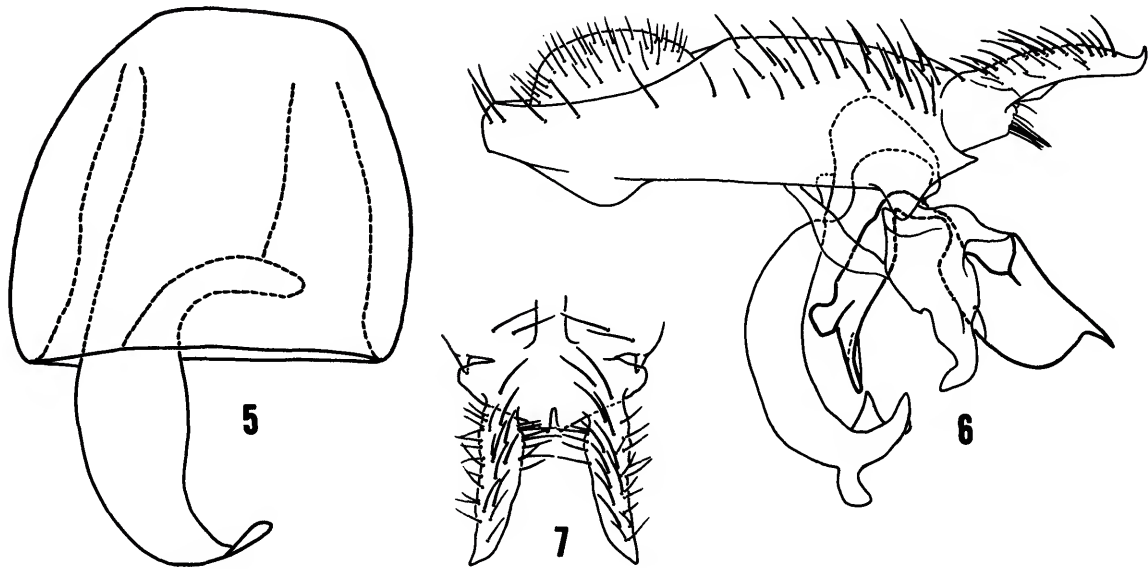
vein M index averaging 1 : 1.1; wing length-to-width ratio averaging 1 : 0.40.

Abdomen: Generally pollinose, grayish blue to grayish brown, each tergum darker anteriorly and along median, becoming more grayish blue toward posterior and lateral margins. Fifth tergum of male slightly longer than fourth, as wide as long.

Male Terminalia (Figures 6, 7): Epandrium more or less parallel sided in caudal view, somewhat flattened in profile, with anteroventral margin distinctly angulate; surstylus a simple, long, slender process with apex slightly recurved; gonite almost as wide as long, narrowing apically to curved point; aedeagal apodeme long, pointed ventrally, dorsal portion broad, curved posteriorly; aedeagus bifurcate (Figure 6), posterior lobe somewhat rectangular, anterior margin rounded, posteroventral corner drawn out to form acuminate narrow process, anterior lobe with ventrolateral process, process enlarged apically, rounded, otherwise lobe tapering ventrally, forming pointed process; hypandrium with long anterior process, anterior portion broadly bifurcating and folded back on itself.

Female Terminalia: Female ventral receptacle (Figure 5) with operculum as high as wide, lateral margins arched, dorsum flat, extending process narrowed apically, slightly curved apically. Segments 6–7 complete; sixth spiracle situated near anteroventral corner of tergum; sixth sternum rectangular, about 3 times longer than wide, slightly wider anteriorly; seventh sternum rectangular, about one and one-half times longer than anterior width, anterior margin distinctly wider. Eighth segment as follows: tergum divided into 2 lateral tergites, each becoming gradually wider ventrally; sternum divided longitudinally, each sternite 3 to 4 times longer than wide, becoming more setose posteriorly, with 3 to 4 apical long setae. Ninth sternum also divided longitudinally, short, each sternite bearing 1 large bristle posteriorly; ninth tergites fused with cerci, each bearing 1 large bristle posteroventally.

DESCRIPTION OF IMMATURE STAGES.—*Egg* (Figure 8): Length 0.70–0.80 mm (\bar{x} = 0.76); max-

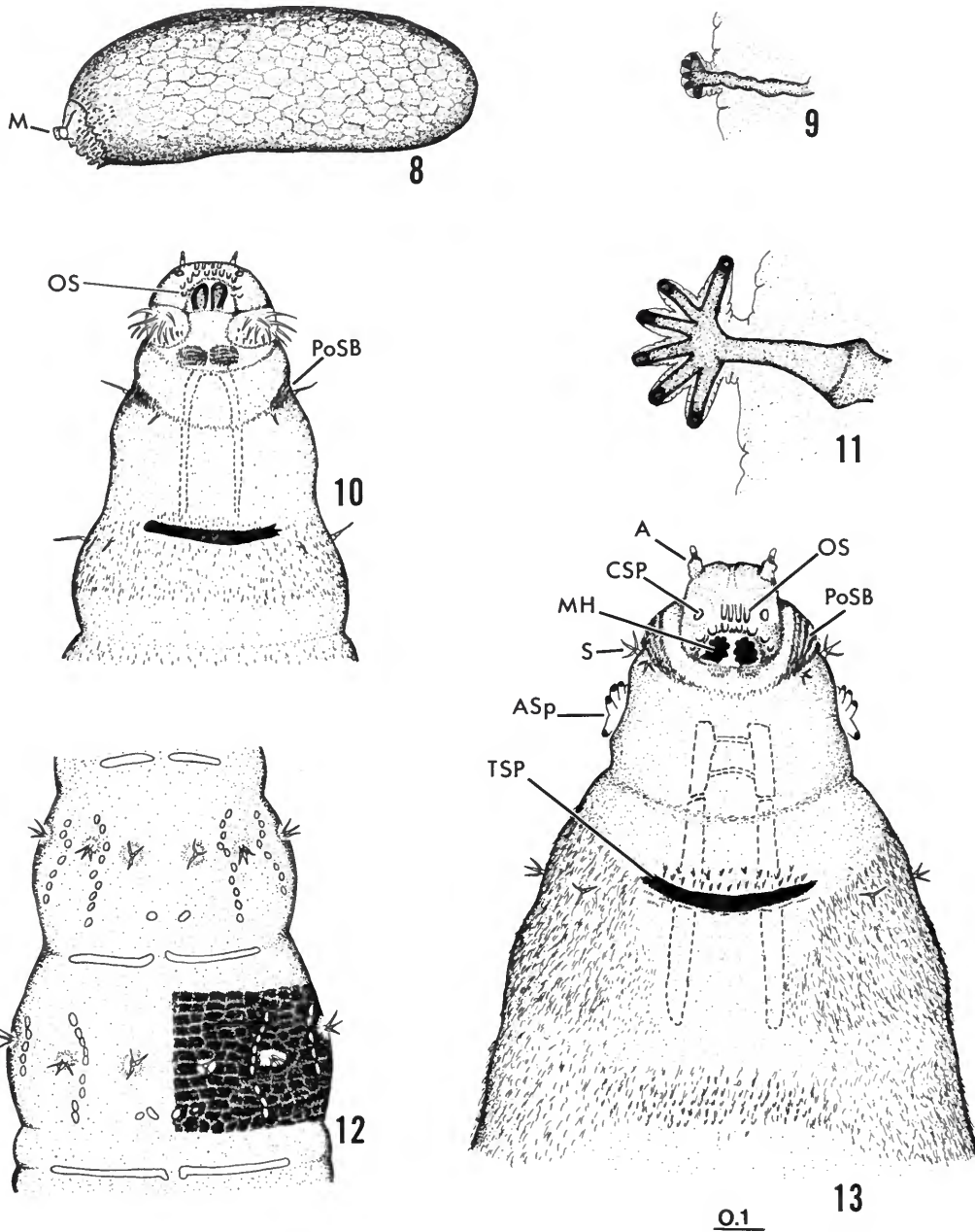


FIGURES 5-7.—*Cirrula austrina*: 5, female ventral receptacle, lateral aspect; 6, male terminalia, lateral aspect; 7, ventral margin of epandrium and surstyli, posterior aspect.

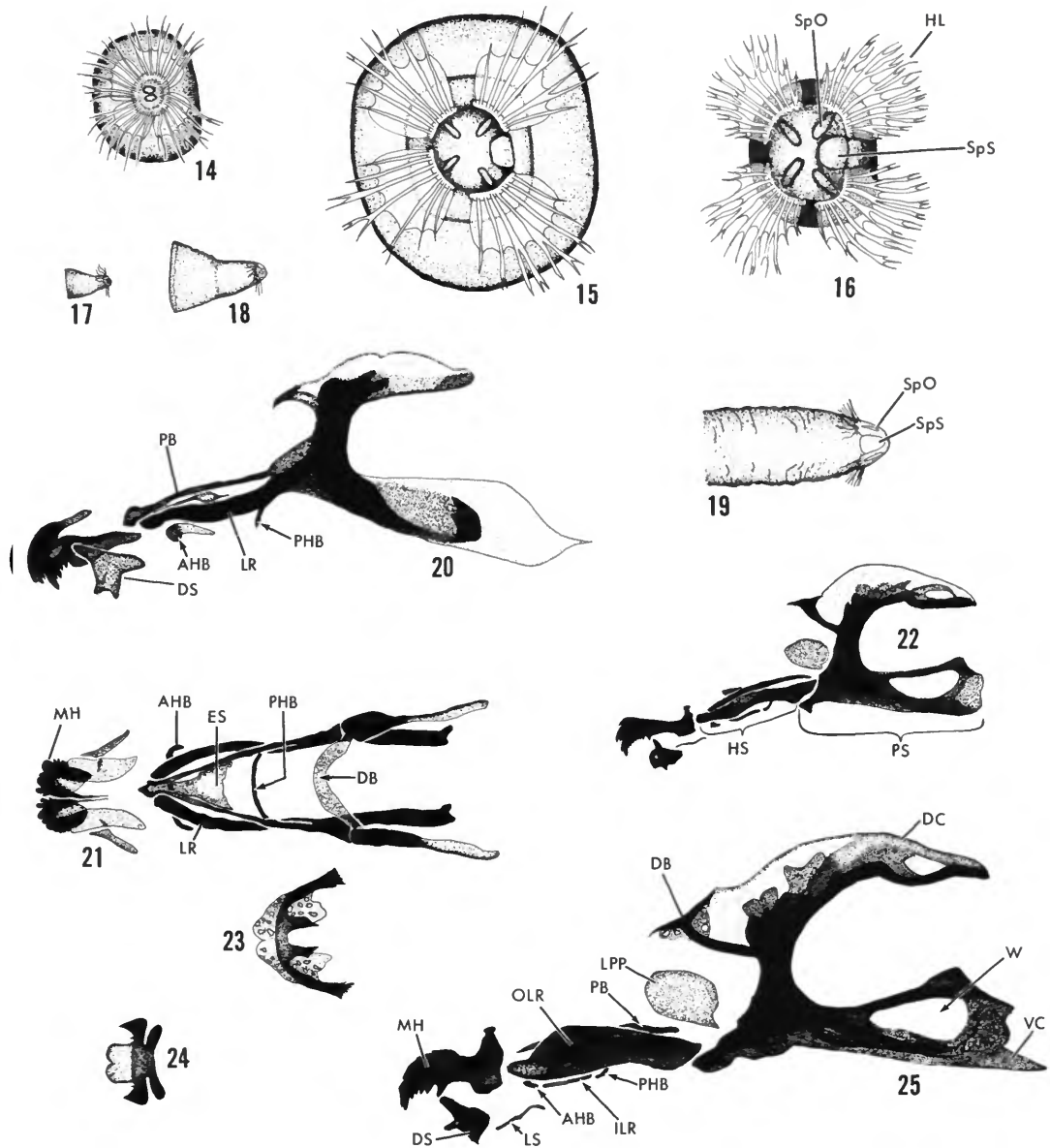
imum width in dorsal view 0.28–0.32 mm (\bar{x} = 0.30). Pale to light pink just after oviposition; becoming cloudy with pink center after 12 hours; larval structures becoming visible through chorion after 36 hours. Ellipsoidal, somewhat flattened ventrally. Chorion surface reticulate with hexagonal pattern, becoming irregular and interspersed with light spines at micropylar end. Micropylar end bluntly rounded; micropyle on pedicel in center of apical circular depression and surrounded by thin, spinelike processes. (Based on 26 specimens, 23 reared and 3 field collected.)

First-Instar Larva: Main body length 1.40–2.28 mm, respiratory tube length 0.24–0.40 mm; maximum width in dorsal view 0.24–0.37 mm. Integument transparent with numerous hairlike spinules and fleshy, unbranched sensilla. Similar to third-instar larva except in the following characters. Segment 1 (Figure 10) with oral spinules smaller and much less pigmented distally; lobes posterolateral to atrium well armed with long, thin spines; antennae entirely pale. Segment 2 with much weaker postoral spine band; small, light hairs on posterior one-third of segment;

anterior spiracles absent. Segment 3 with scattered light hairs; sensilla unbranched. Segments 4–11 with sparse hairs; dorsal patterns absent; sensilla reduced and unbranched; tubercles not evident. Crochets on prolegs lighter; crochets of anterior row one-third larger than those of second row; those of posterior row very small; 3 obvious rows of crochets on terminal proleg. Posterior spiracular caps (Figures 14, 17) lightly pigmented; each hydrofuge lamella with fewer apical branches in each group; 2 moderately distinct spiracular openings; spiracular scar absent (Figure 14). Cephalopharyngeal skeleton (Figures 20, 21) length 0.27–0.32 mm; generally less pigmented. Mouthhooks lightly pigmented except along distal edges; medial and lateral edges each tapering to a fine point posteriorly. Ligulate sclerite absent; dentate sclerite present and well developed. Inner and outer longitudinal rods (subhypostomal sclerites) of hypostomal sclerite fused together. Epistomal sclerite lightly pigmented, gradually expanded posteriorly; parastomal bars and hypostomal sclerite fused to pharyngeal sclerite. Pharyngeal sclerite without anterolateral pro-



FIGURES 8-13.—*Cirrula austrina*: 8, egg, lateral aspect; 9, anterior spiracle of second-instar larva, lateral aspect; 10, first-instar larva, anteroventral aspect; 11, anterior spiracle of third-instar larva, lateral aspect; 12, segments 3 and 4 of third-instar larva, dorsal aspect; 13, third-instar larva, anteroventral aspect. (Abbreviations in "Methods.")



FIGURES 14-25.—*Cirrula austrina*: 14, posterior spiracular cap of first-instar larva, posterior aspect; 15, same of second-instar larva, posterior aspect; 16, same of third-instar larva, posterior aspect; 17, same of first-instar larva, lateral aspect; 18, same of second-instar larva, lateral aspect; 19, same of third-instar larva, median aspect; 20, cephalopharyngeal skeleton of first-instar larva, lateral aspect; 21, same, dorsal aspect; 22, same of second-instar larva, lateral aspect; 23, dorsal bridge of third-instar larva, dorsal aspect; 24, epistomal sclerite of third-instar larva, dorsal aspect; 25, cephalopharyngeal skeleton of third-instar larva, lateral aspect.

cesses; dorsal bridge lightly pigmented and not reticulate; ventral cornua without windows. (Based on 9 reared specimens.)

Second-Instar Larva: Main body length 2.33–4.92 mm, respiratory tube length 0.58–0.91 mm; maximum width in dorsal view 0.42–0.83 mm. Similar to third-instar larva except in the following characters. White to grayish white; integument transparent with numerous small spines, most obvious dorsally. Spines smaller and lighter than those of third-instar larva, no dorsal patterns; sensilla somewhat more obvious, often with dark tips. Anterior spiracles (Figure 9) with 5–6 less distinct marginal papillae, moderately pigmented. Posterior spiracular caps (Figures 15, 18) moderately pigmented, dark basally, subtriangular and constricted near the middle; each hydrofuge lamella composed of fewer, shorter hairs. Cephalopharyngeal skeleton (Figure 22) length 0.44–0.46 mm; generally less pigmented. Hook part of mouthhook basally with strong anteroventral tooth. Parastomal bars nearly free from hypostomal sclerite. Pharyngeal sclerite more closely appressed to hypostomal sclerite; dorsal cornua with 1 or more faintly pigmented windows. (Based on 13 specimens, 10 reared and 3 field collected.)

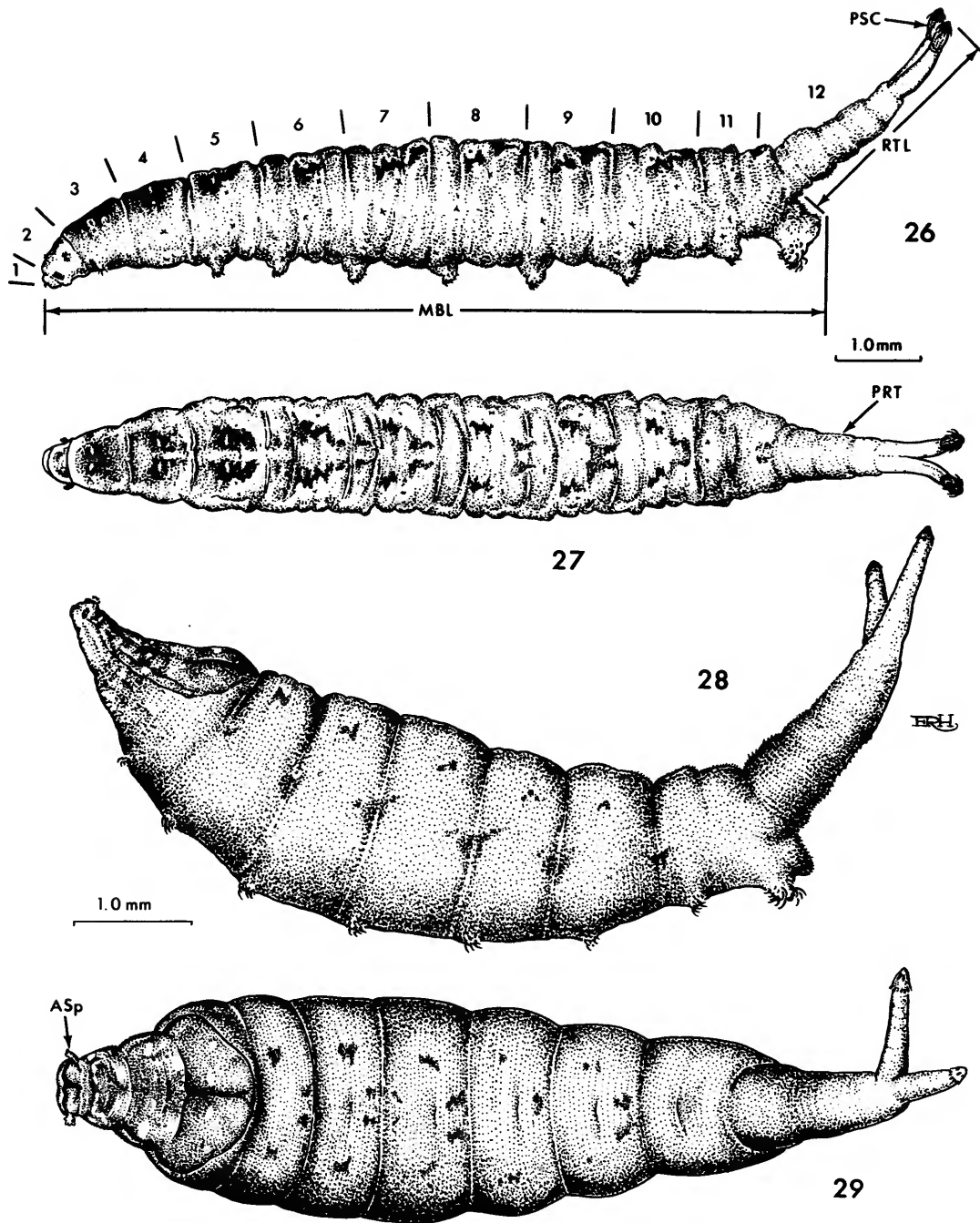
Third-Instar Larva (Figures 26, 27): Main body length 6.25–10.25 mm, posterior respiratory tube length 1.41–2.58 mm; maximum width in dorsal view 1.17–1.58 mm. Internal structures mostly white, integument transparent with numerous spinules, spines, and scales. Shape cylindrical, tapering somewhat anteriorly; first 2 segments retractile, evaginated or invaginated in preserved specimens; caudal segment elongated to form posterior respiratory tube, telescoping and branching distally. Segment 1 (pseudocephalic) bilobed anteriorly; each lobe with small, 3-segmented antenna directed anterodorsally, segments 1 and 3 pale, segment 2 light brown; circular sensory plate on each lobe ventral to antenna (Figures 13, 31, 32); facial mask with row of 4 subequal comblike oral spinules between sensory plates, light to dark brown apically; second row of 8 slightly larger spinules posterior to

first, just anterior to atrium (mouth opening); additional oral spinules in 2–3 indefinite lateral rows on each side of atrium and extending into buccal cavity (Figure 13). Evaginated specimens (Figure 30) with spinose lobe on each side posterolateral to atrium; 2 patches of minute spinules arranged in rows posteromedially. Invaginated specimens (Figure 31) with posterolateral spinose lobes not evident, contained within buccal cavity; patches of minute spinules bordering atrium posteriorly. Segment 2 (prothoracic) with postoral spine band weak anteroventrally, widening laterally into well developed spine patches consisting of dark spines arranged in definite rows, and absent dorsally; remainder of segment with uneven rows of peglike structures, subrectangular spine patch dorsally; banded on anterior one-third by 10 trilobed sensilla; anterior spiracles laterally near posterior border, palmate, usually with 6 marginal papillae (may also be 4, 5, or 7), dark at tips (Figures 11, 33). Segments 3–5 heavily spinose dorsally and laterally; spines interrupted on these 3 segments by small, oval, glabrous patches, arranged in 2 arcs on each side dorsolaterally (Figure 12). Segment 3 (mesothoracic) heavily spinose; 10 trilobed sensilla (Figure 34) near anterior one-third; dark transverse strap at anteroventral border (Figure 13); remainder of segment with scattered lighter spines. Segment 4 (metathoracic) heavily spinose; dorsally with 2 indistinct dark patches formed by flattened, scale-like spines; lateral and ventral areas less spinose; banded midway by 10 small tubercles, each bearing trilobed sensillum centrally. Segments 5–11 (1–7 abdominal) spinose, more or less with 3 annuli, variously wrinkled and tuberculate; each bearing ventral proleg; dorsal patterns present, consisting of flattened, scalelike spines, reduced or absent on segments 10 and 11. Dorsal tubercles small, 3 per side, 1 bordering pattern medially and 2 laterally; each bearing trilobed sensillum centrally. Remainder of each segment moderately and evenly spinose. Two lateral tubercles arranged vertically above each proleg, each with trilobed sensillum centrally. Prolegs well developed, slightly bilobed; all subequal except slightly

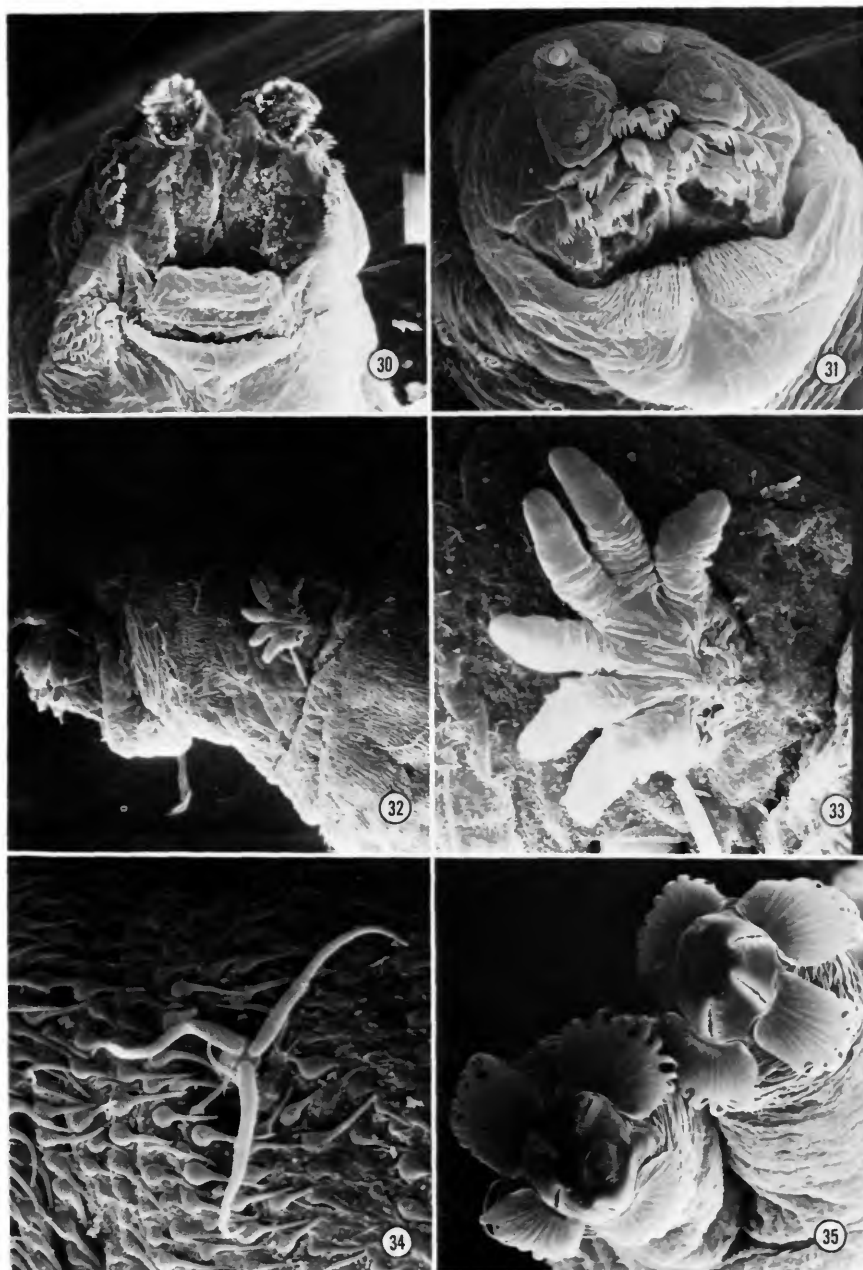
smaller on segment 5. Lobes of prolegs each with 3 distinct rows of long, stout, curved spines, (hereafter referred to as crochets). Crochets directed posteriorly; anterior row largest, 4 crochets per side; crochets of second row $1/2$ – $2/3$ as large, 4 per side; 1 smaller crochet laterally between rows 1 and 2; crochets of third (posterior) row much smaller, 4–6 per side. Segment 12 with dorsal pattern reduced or absent; bearing posterior respiratory tube distally and large, subcylindrical proleg ventrally (the anal or terminal proleg). Four rows of crochets anterodistally on proleg, slightly tapering laterally and divided medially by small cleft; directed anteriorly; crochets of posterior row largest, 5 per side; crochets of third row somewhat smaller, 5 per side; crochets of most anterior row much smaller, 5 or more per side. Perianal pad apical on proleg; subcircular, somewhat bilobed posteriorly and glabrous; small patch of small, dark spinules at medioposterior border; anus longitudinal in middle of pad. Respiratory tube spinose at base, tapering and slightly less spinose distally; branches bearing spiracles without spines; paired ventrolateral tubercles bearing trilobed sensilla on basal one-fifth; 2 similar sensilla near middle. Posterior spiracular caps (Figures 16, 19, 35) light to dark brown, bluntly pointed apically; 4 elongate ellipsoidal spiracular openings apically, each bordered basally by a broad, hydrofuge lamella; each lamella split into 10 or more pale branching areas apically; spiracular scars located medially, facing one another, each scar rounded and lightly pigmented. Cephalopharyngeal skeleton (Figure 25) length 0.68–0.80 mm, mostly darkly pigmented. Mouthhooks paired, not interconnected, length 0.12–0.14 mm; hook part of each mouthhook slightly decurved, rounded and spatulate, toothed laterally and apically, median edge with teeth slightly larger; without windows; basal part with weak lateral flange apically and bluntly rounded dorsal projection. Dentate sclerite located ventrolateral to mouthhook on each side. Ligulate sclerite paired, each piece long and thin, with 2 or more small, angular bends; posterior part lying beneath anterior edge of hypostomal sclerite, di-

rected anteriorly toward midline. Hypostomal sclerite paired, length 0.24–0.29 mm, composed of 2 pairs of longitudinal sclerites (rods) and 2 transverse bridges; each outer longitudinal rod stoutest at junction with parastomal bar, anteroventral portion expanded laterally to articulate with mouthhook; anterior hypostomal bridge intersecting anterior one-fourth of outer longitudinal rods, thin, slightly curved and bowed ventrally; posterior hypostomal bridge intersecting posterior one-third of outer longitudinal rods, much like anterior bridge but more strongly bowed; inner longitudinal rods articulating with anterior and posterior bridges, angled near midlength, slightly diverging posteriorly. Epistomal sclerite strongly convex, mostly darkly pigmented, bracing outer longitudinal rods of hypostomal sclerite dorsomedially; shaped as figured (Figure 24). Pharyngeal sclerite length 0.36–0.40 mm; indentation index 67–73; anteroventral edge ventral to and free from hypostomal sclerite; paired lateral pharyngeal processes rounded, flat, disclike and free from main pharyngeal sclerite; dorsal bridge highly reticulate (Figure 23); dorsal cornua with small posterior window; ventral cornua with subovate to subtriangular window posterodorsally. (Based on 23 specimens, 4 reared and 19 field collected.)

Puparium (Figures 28, 29): Main body length 5.56–7.89 mm (\bar{x} = 6.83), breathing tube length 2.41–3.32 mm (\bar{x} = 2.85), maximum width in dorsal view 1.74–2.41 mm (\bar{x} = 2.14). Yellowish brown to brown; translucent to moderately transparent; entirely rigid. Venter generally arcuate in lateral view, dorsum flattened; anterior end flattened dorsally and tapering; posterior end elongate. Segment 1 and most of segment 2 invaginated. Anterior spiracles arising just behind anterolateral corner of puparium, slightly diverging; usually with 6 marginal papillae. Dorsal cephalic cap delineated by line of weakness extending laterally along segments 2–5, strongly indented near posterior margin of segment 4, transversing segment 5 dorsally near its posterior margin. Ventral cephalic cap delineated by line of weakness transversing segment 5 near its midlength, proleg



FIGURES 26-29.—*Cirrula austrina*: 26, third-instar larva, lateral aspect; 27, same, dorsal aspect; 28, puparium, lateral aspect; 29, same, dorsal aspect.



FIGURES 30-35.—*Cirula austrina*: 30, third-instar larva, anteroventral aspect, evaginated; 31, same, anteroventral aspect, invaginated; 32, same, anterolateral aspect; 33, anterior spiracle of third-instar larva, lateral aspect; 34, sensillum of third-instar larva, lateral aspect; 35, posterior spiracular caps of third-instar larva, posterior aspect.

of segment (P_1) borne on cap. Markings similar to those described for third-instar larva; sensilla not evident. Segments 6–11 with intersegmental indentations strongest dorsally, becoming faint creases ventrally. Prolegs on segments 5–11 flat to weakly protruding. Segment 12 with slightly darker, subovate to ellipsoidal perianal pad ventrally and greatly elongated, distally branching breathing tube posteriorly. Respiratory tube evenly upcurved with ventrolateral tubercles on basal one-fifth; branches diverging between 0° and 90° ; posterior spiracular caps more darkly pigmented than those on mature larvae, structures less discernible. (Based on 11 specimens, 3 reared and 8 field collected.)

TYPE MATERIAL.—Lectotype male [here designated] of the senior synonym is labeled: "Fl[orid]a. [Georgiana]/Collection, C. V. Riley [Mr. William Wittfeld, collector]/Type No. 4299 U.S.N.M. [number handwritten, red]/Ephydra austrina Coq. [handwritten, black bordered]/Dimecoenia austrina A. Coq. [handwritten, black bordered]/Cirrula austrina (Coquillett) Det. W. N. Mathis 1979 [handwritten, black bordered]." Six paralectotypes [here designated] have the same locality data as the lectotype. Coquillett's original description of *S. austrina* listed nine syntypes; apparently two are lost. The lectotype is pinned directly, is in fairly good condition (slightly dirty, dorsum of thorax partially split), and is deposited in the National Museum of Natural History, Smithsonian Institution, USNM type number 4299. The lectotype female [here designated] of the junior synonym is labeled: "Brownsville, Texas [Charles Dury, collector] apr 12 may 20 [1903]/TYPE [red]." The latter lectotype is in the Ohio State University insect collection, Columbus; apparently it is the only extant specimen of the original syntype series.

OTHER SPECIMENS EXAMINED.—MEXICO. NAYARIT: Isabel Island, 24 May 1925, H. H. Keifer (5♂; USNM). SONORA: San Jose Beach, 40 mi SE Obregon, 18 May 1961, Howden and Martin (3♀; CNC). UNITED STATES. ALABAMA: Mobile Co., Coden, 2 Oct 1916 (2♂, 4♀; USNM). CALIFORNIA: Alameda Co., 26 Oct 1968, R. S. Lane (1♂, 1♀; CAS); Albany, hatched in Laboratory, 12 Mar 1921, C. T. Dobbs, B. Brookman (2♂, 3♀; CAS). Marin Co., Mazaneto,

27 Oct 1907, Bradley (1♂, 1♀; CU). Orange Co., Corona del Mar, 16 May–11 June 1944–1949, A. L. Melander (2♂, 1♀; USNM); Laguna, 1 Aug 1932, J. M. Aldrich (1♀; USNM); Newport Beach, 27 Oct 1928 (2♀; USNM); Santa Ana, 31 Mar 1961, J. Bath (1♂; CU). San Diego Co., San Diego, 5 Apr 1915, M. C. Van Duzee (5♂, 3♀; CAS). San Luis Obispo Co., Morro Bay, 30 Aug 1945, A. L. Melander (1♂; CAS). Santa Clara Co., Palo Alto, 20–26 Apr 1906, J. M. Aldrich (10♂, 1♀; USNM); San Jose Beach, 40 mi SW Obregon (1♂; USNM). FLORIDA: Broward Co., Hollywood, 12 May 1967, B. V. Peterson (2♂, 1♀; CNC). Charlotte Co., Punta Gorda, 12 Apr 1952, J. R. McGillis (1♀; CNC). Collier Co., Everglade, 15 Apr 1912 (2♂, 2♀; AMNH). Dade Co., Biscayne Bay (1♀; AMNH); Homestead, Subtropical Experiment Station, 2 May 1967, B. V. Peterson (1♀; CNC); Miami, 3 Mar 1938, C. T. Green (1♂, 1♀; USNM). Highland Co., Archbold Biological Station, 20 Apr–23 Apr 1947–1967, J. G. Needham, B. V. Peterson (5♀; CNC, CU). Indian River Co., Sebastian, 9 Feb 1919, A. Wetmore (4♂, 1♀; USNM). Lee Co., Sanibel Island, 11 May 1973, W. W. Wirth (2♀; USNM). Monroe Co., Cape Sable, 24 Mar–25 Apr. 1953–1955, K. V. Krombein, H. E. Evans (3♂, 6♀; CU, USNM); Flamingo, 25 Jan–7 May 1939–1967, A. L. Melander, B. V. Peterson (9♂, 19♀; CNC, USNM); Key Largo, 25 Jan–4 Apr 1932–1966, A. L. Melander, H. V. Weems (3♂, 2♀; CU, USNM). Palm Beach Co., Lake Worth, Slosson (1♂, 1♀; AMNH, USNM). LOUISIANA: Calcasieu Par., Sabine River Ferry, 20 Jun 1917 (2♂, 1♀; CU). MISSISSIPPI: Jackson Co., Ocean Springs, Gulf Coast Research Laboratory, 14 Jun 1962, D. L. Deonier (2♂, 1♀; DLD, USNM). TEXAS: Padre Island near Pt. Aransas, 23 Mar 1965, J. G. Chillcott (1♂; CNC). Cameron Co., Brownsville, 12 Apr–20 May (2♀; AMNH, USNM). Galveston Co., Galveston, 11 Feb–Jun 1900–1932, L. D. Tuthill (1♂, 1♀; USNM). VIRGINIA: Accomack Co., Assateague Island, Tom's Cove, 25 June–12 Aug 1970–1971, K. W. Simpson (13♂, 9♀; CU); Chincoteague Island, salt marsh, 25 Jun 1970, K. W. Simpson (8♂, 3♀; CU); Cackle Creek, 0.2 mi W, salt marsh, 1–13 Aug 1970–1971, K. W. Simpson (2♂, 5♀; CU); Eel Creek Marsh, E of Chincoteague, 13 Aug 1971, K. W. Simpson (4♂, 12♀; CU). Virginia Beach, 14 Aug 1913, Knab (1♂; USNM).

GEOGRAPHIC DISTRIBUTION (Figure 36).—*Cirrula austrina* occurs on both the Atlantic and Pacific coasts of North America below 40° north latitude. Steyskal (1970) recorded this species as far south as Isabel Island (Mexico, off the coast of the State of Nayarit). Wirth (1965) also listed a record from Bermuda.

NATURAL HISTORY.—Along the coast of southeastern United States, this species occurs commonly in or on mats of filamentous algae in salt marshes. Adults are strong fliers and commonly

fly several yards when disturbed, although they could be collected in abundance by sweeping just above the mats. Populations seemed to reach their highest densities where the habitat had partially dried, rendering firmer mats and leaving them on solid ground (Figures 115, 116).

Courtship behavior was observed on two days in the field, the 12th and 13th of August, 1971. As a female was approached by a male, she flicked both wings quickly every few seconds. After approaching slowly, the male extended one wing perpendicularly for one or two seconds, then returned it to its normal position. After repeating this process a few times, he maintained the wing in its extended position and circled behind the female in such a way that the tip of the extended wing was always quite close to her. The male then mounted the female from behind and was either allowed to copulate or was rejected. Both copulation and rejection were followed by a posterior dismounting and short wing spreading display.

Specimens to be reared were collected in Virginia, Accomack County, at the following locali-

ties and dates: Chincoteague National Wildlife Refuge, Tom's Cove and vicinity, 25 June 1970 and 9 August 1970; Eel Creek Marsh, 12 August 1971 and 30 May 1972; Route 175, 0.5 mi W Cackle Creek, 9 August 1970, 12 August 1971, and 30 May 1972.

Adults maintained in the laboratory fed readily on field-collected salt marsh algae, occasionally supplemented with a honey and brewers' yeast paste. Field-collected males lived 11–18 days in laboratory colonies; females, 11–25 days. Laboratory-reared adults usually died within seven days of emergence.

In the laboratory, eggs were laid in various moist substrates but were concentrated in salt marsh algae when the latter was provided. Oviposition was not observed directly in nature, but a cluster of six eggs was recovered from a field-collected algal mat. Eggs were usually found in crevices or folds in the algae, located either on top of or just beneath the surface. Maximum recorded egg production for this species was 125 eggs over a six day period; the maximum daily output, 32 eggs. The incubation period at room

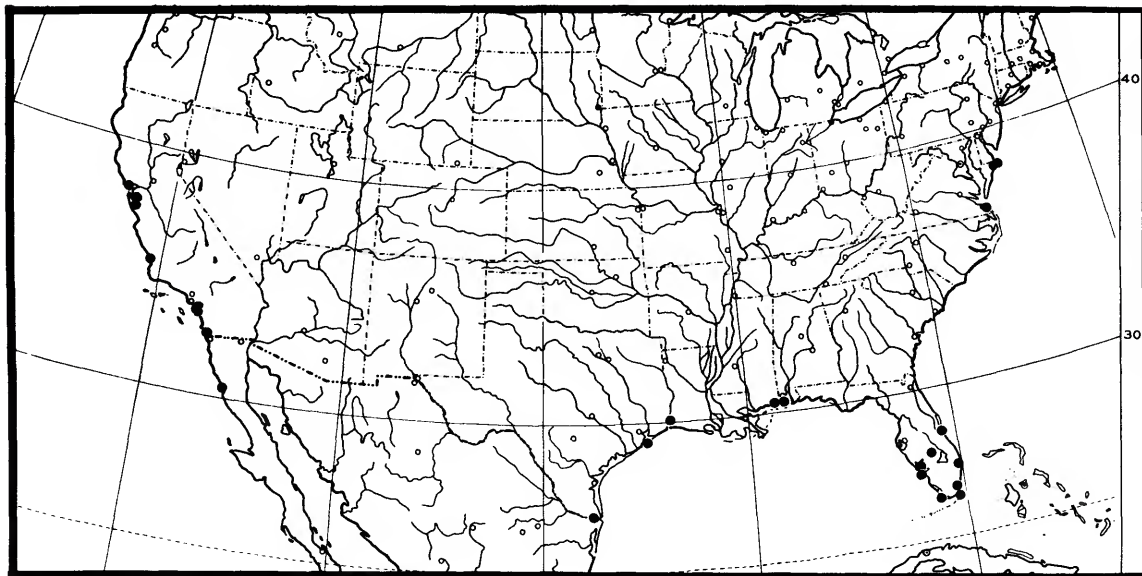


FIGURE 36.—Distribution map of *Cirrula austrina*.

temperature was two to three days, with 12 of the 20 observed eggs hatching on the third day. Newly hatched larvae began feeding as soon as they found a suitable food source. The first stadium lasted three days (18 observations); the second, three to seven days (15 observations); and the third, 14–20 days (8 observations).

The larvae are basically infraneustonic, living within the top centimeter or so of the substrate and keeping their posterior spiracles in more or less constant contact with the air-water interface. The ventral prolegs are well adapted for helping the larva to move through tangled masses of filamentous algae. The dorsal spine patterns may also aid in locomotion by snagging strands of algae beneath the flattened scalelike spines (Simpson, 1979).

The posterior spiracles are periodically pulled beneath the surface, usually to enable the larva to move about freely within the substrate, but they remain beneath the surface for only a few seconds at a time. As the spiracles are submerged, the hydrofuge lamellae converge around the peritreme and envelop it in an air bubble. In this manner the tracheal system is protected from contamination by water and dirt. Some larvae of *Ephydra* remain submerged for long periods of time, utilizing the air bubble as a plastron to supplement cuticular respiration (Aldrich, 1912; Ping, 1921). There is no indication that larvae of *Cirrula austrina* have this capability.

All known larvae of Ephydrini share the same feeding habits, being microphagous (Simpson, 1979). The larval mouthhooks, including those of *C. austrina*, are scoop shaped and are well adapted for directing liquid or semi-liquid materials into the mouth. Several rows of comblike spinules surround the mouth and act in conjunction with the mouthhooks to filter particulate material from the water. As the mouthhooks are extended, these structures flare outwards (Figure 30). As the mouthhooks are withdrawn, these structures collapse around the mouth, straining particulate matter from the aqueous medium in the process (Figure 31). The larva further concentrates the particulate matter through the use of pharyngeal

ridges, located on the floor of the pharynx. The roof of the pharynx is forced downward against the ridges, forcing excess water between the ridges. The larva then expels the water through its mouth and swallows the particulate matter which was retained above the ridges. This mechanism is common among microphagous maggots and was described in detail by Dowding (1967).

While the larvae are feeding, the mouthhooks can be seen moving in and out of the mouth at a rate of several (2–3) times per second. The larvae feed almost continuously, ceasing for extended periods only when they are about to molt or pupariate.

Pupariation occurs just beneath the surface of the substrate, with the posterior respiratory tube projecting above the surface and the cephalic cap located just beneath the surface. The main portion of the puparium usually is concealed beneath a thin layer of the substrate. Because the puparium is located close to the surface, the adult merely crawls out of the puparium and onto the substrate when it emerges. In laboratory rearings, adults emerged seven to nine days after the puparium had formed (7 observations).

Cirrula gigantea Cresson

FIGURES 37–61, 112, 117

Cirrula gigantea Cresson, 1917:71.—Sturtevant and Wheeler, 1954:162 [review].—Wirth, 1965:753 [catalog].

Pogonephydra chalybea Hendel, 1917:42; 1931:10 [synonymy].

DIAGNOSIS.—Specimens of *C. gigantea* may be distinguished from those of *C. austrina* by the following combination of character states.

Adults: Laterocline fronto-orbital bristles short; cruciate intrafrontal bristles short, less than one-half length of arista, not overlapping apically; parafrons blackish brown, densely pollinose, appearing velvety; arisal rays short, less than arisal width at base; face with dense patch of long bristles subdorsally, just below interfoveal carina; dorsocentral bristles with only posterior pair well developed, anterior 4 pairs barely discernible from surrounding setulae; presutural

bristle weakly developed, less than one-half length of anterior notopleural bristle; tarsi of front leg of male broadly explanate; hypandrium weakly sclerotized; setae of epandrium around cercal cavity conspicuously more dense and longer than other setae.

Third-Instar Larva: Transverse sclerotized strap of third segment approximately 6 times as wide as long and with posterior projection, somewhat lighter colored; overall length of larva up to 17.5 mm; cephalopharyngeal skeleton 0.9–1.0 mm in length.

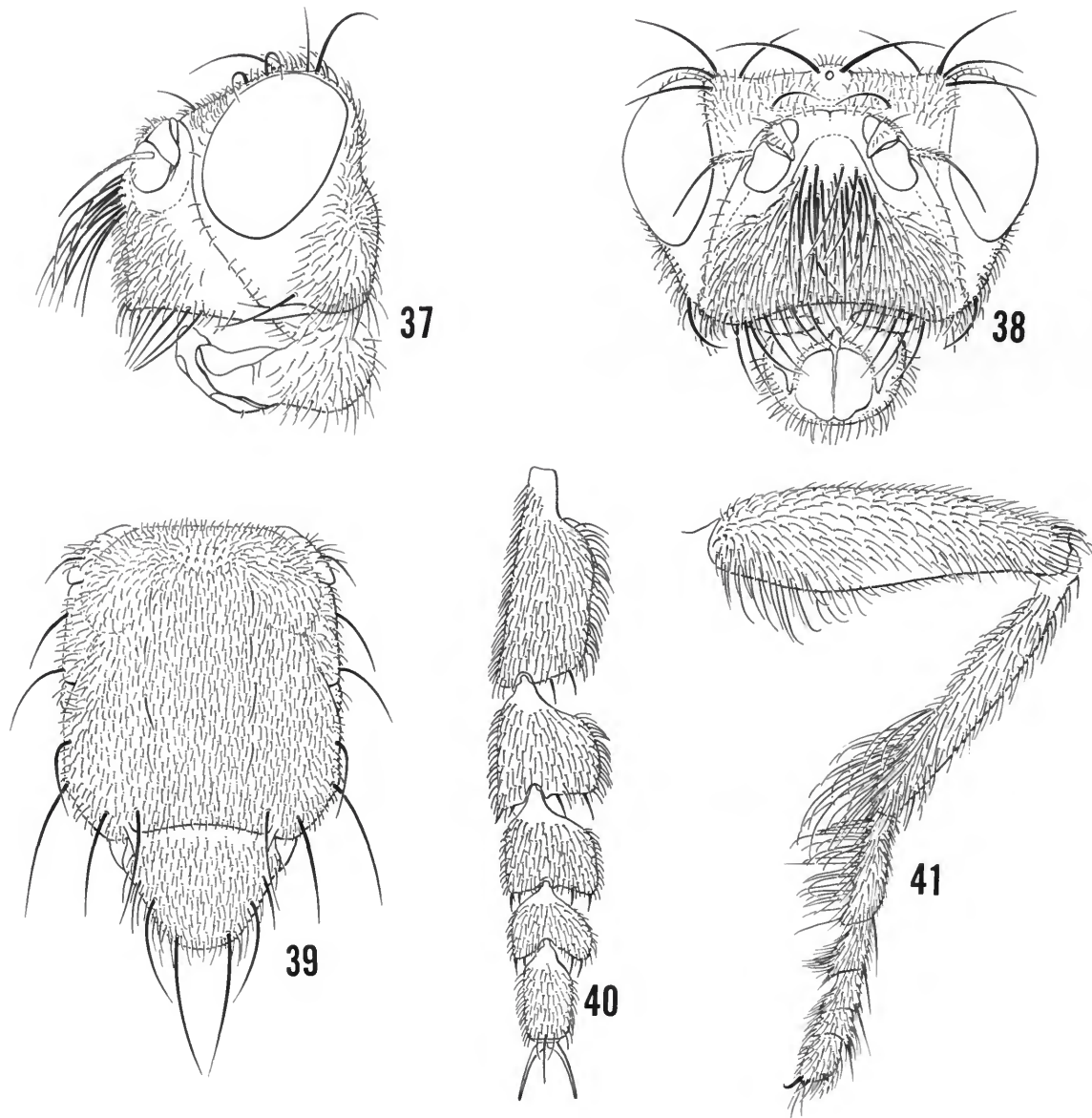
DESCRIPTION OF ADULT.—Large shore flies, length 5.81 to 8.52 mm; mostly dull, olivaceous brown to grayish green, with subshiny to shiny areas on dorsum.

Head (Figures 37, 38): Head width-to-height ratio averaging 1 : 0.65; frons width to length ratio averaging 1 : 0.74; mesofrons with median shallow depression between median ocellus and ptilinal suture, shiny, with deep metallic greenish blue luster, median depression appearing more pollinose because of depression angle; intrafrontal bristles convergent but not cruciate, short, at most equal to combined length of first 2 antennal segments; remainder of mesofrons with small setulae; ocellar triangle and parafrons pollinose, ocellar triangle blackish brown; parafrons blackish, appearing velvety; ocelli arranged in equilateral triangle; laterocline fronto-orbitals small, less than combined length of antenna; postocellar setae mostly small, length no longer than distance between ocelli; postocular setae uniform in size, generally small. Antenna mostly unicolorous, brown to blackish brown; arista about as long as combined length of first 3 antennal segments, basal third to half more or less uniformly thickened, ending abruptly, apical one-half to two-thirds, slender, stylelike, longest arisal rays not greater than arisal width at base. Face width-to-height ratio averaging 1 : 0.79; interfoveal carina prominent, dorsolateral margins angled sharply, dorsum shiny, mostly concolorous with mesofrons, with dense patch or patches (somewhat divided medially) of well-developed bristles just below dorsum of interfoveal carina, other facial

setae weak except along oral margin; antennal fovea deeply depressed, coloration similar to remainder of face, grayish brown to brown, slightly darker dorsally, with some olivaceous color laterally; oral margin shallowly emarginate toward middle. Eye width-to-height ratio averaging 1 : 1.24; eye-to-cheek ratio averaging 1 : 0.44; gena moderately high, mostly bare directly below eye but with a row of setae along anterior margin of parafacies and several setae posteriorly, the latter becoming more well developed posteroventrally; gena more or less concolorous with face, more olivaceous.

Thorax (Figure 39): Mesonotum dull to subshiny, becoming darker and shinier posteriorly; with longitudinal pollinose vittae between subshiny ones, these more evident anteriorly, color olivaceous to brown, subshiny areas with metallic greenish blue luster; acrostichal setae uniseriated; dorsocentral bristles 5 pairs, anterior 4 pairs much reduced, only slightly larger than surrounding setulae, posterior pair well developed; presutural bristle reduced, generally inconspicuous. Pleural areas lighter and more densely pollinose than dorsum; mesopleuron and pteropleuron more or less concolorous, olivaceous brown, sternopleuron mostly grayish, especially anteriorly, becoming lightly olivaceous brown posteriorly. Legs generally dark colored, dull densely pollinose, sexually dimorphic; dorsum of femora grayish green, becoming more brownish laterally and ventrally; tibiae nearly concolorous with femora, except becoming conspicuously darker apically, blackish; tarsi black; hind femora of male turgid (Figure 41); hind tibiae of male with apicoventral patch of long setae; hind tarsi moderately explanate, bearing a row of long setae along anterior margin, especially evident on basitarsus; front tarsi of male (Figure 40) conspicuously explanate posteriorly. Wing (Figure 112) length averaging 5.7 mm; generally subhyaline to lightly infuscated, light brown; costal vein index averaging 1 : 0.18; vein M index averaging 1 : 0.95; wing length-to-width ratio averaging 1 : 0.44.

Abdomen: Subshiny to shiny, sparsely pollinose; olivaceous to distinctly bronzy. Fifth ter-

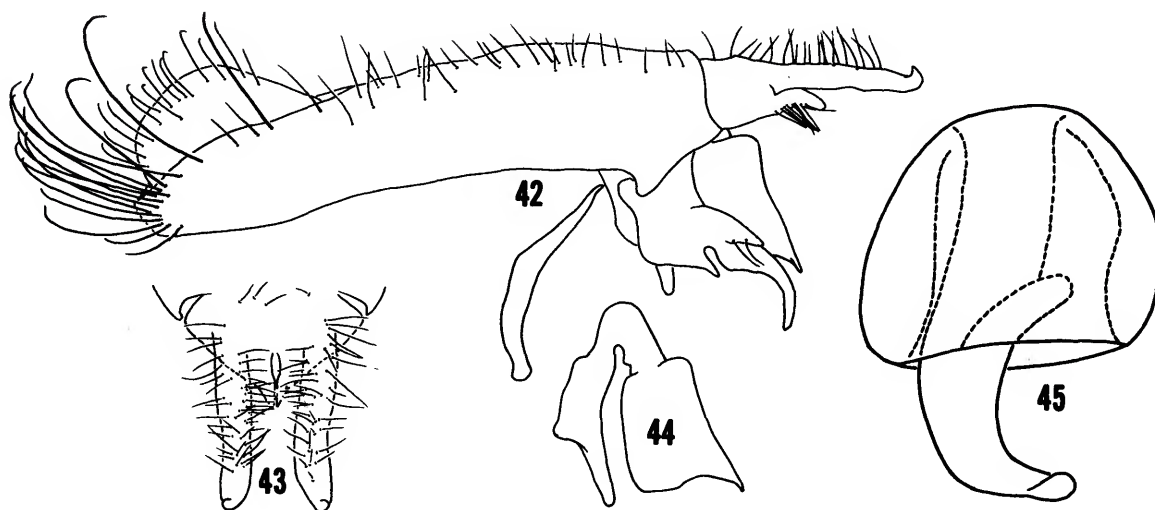


FIGURES 37-41.—*Cirrula gigantea*: 37, head, lateral aspect; 38, same, anterior aspect; 39, thorax, dorsal aspect; 40, tarsi of front leg of male, dorsal aspect; 41, hind leg of male, lateral aspect.

gum of male longer than basal width, triangular, apical setae larger especially along margin.

Male Terminalia (Figures 42-44): Epanthrium more or less parallel sided in caudal view, slightly broader medially, comparatively flattened in pro-

file, with anteroventral angulation; surstylus digitiform, 4 to 5 times longer than wide, recurved apically to corniform apex; gonite complicate basally (Figure 42), apically forming lunate process; aedeagus bifurcate, posterior lobe with api-



FIGURES 42-45.—*Cirrula gigantea*: 42, male terminalia, lateral aspect; 43, ventral margin of epandrium and surstyli, posterior aspect; 44, aedeagus, lateral aspect; 45, female ventral receptacle, lateral aspect.

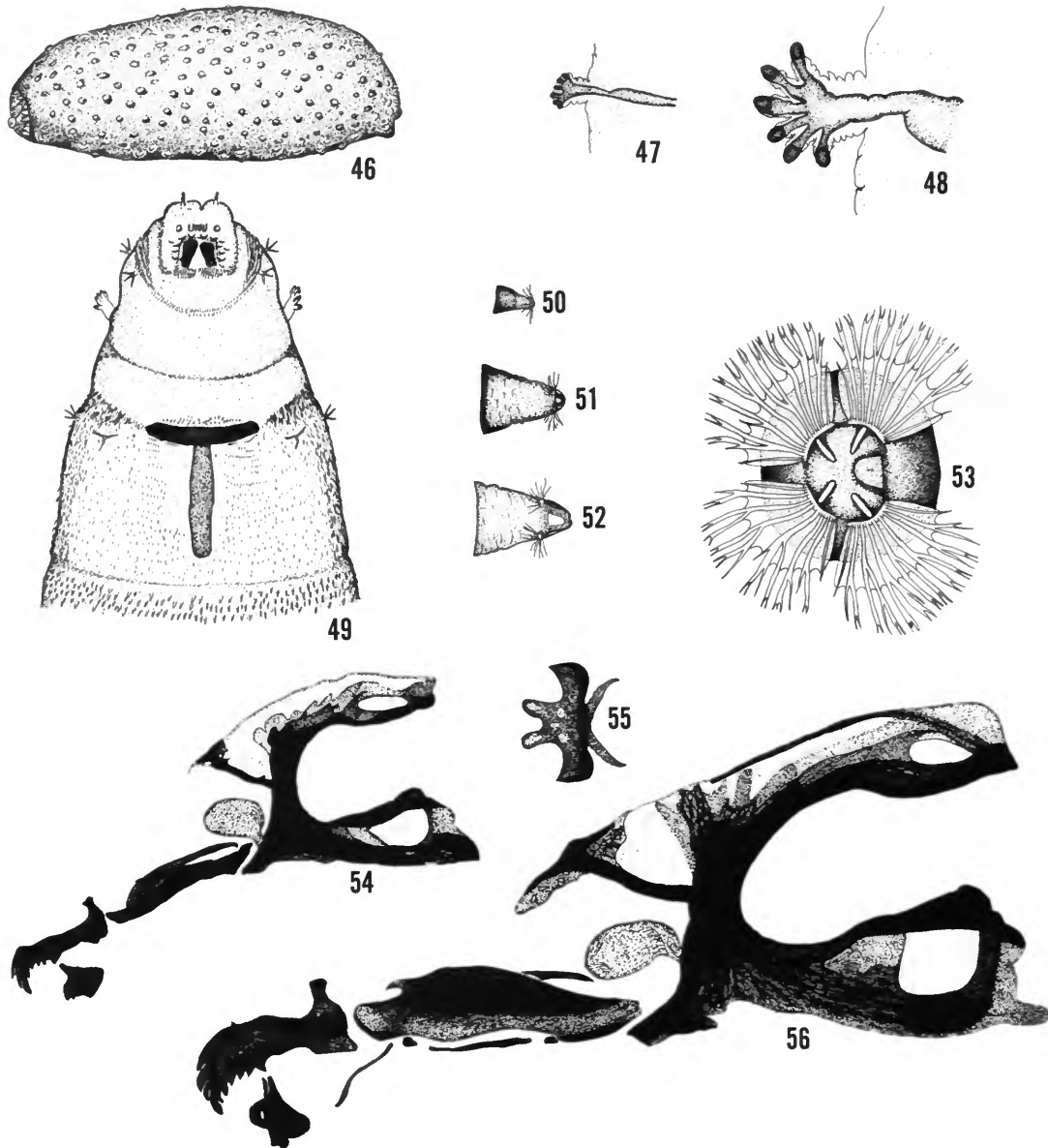
cal two-thirds more or less rectangular, posteroventral corner forming acuminate narrow tip, anterior lobe as long as posterior lobe, basal two-thirds parallel sided, apical one-third abruptly narrowing to tapering narrow process, rounded apically; hypandrium with poorly sclerotized anterior ribbon; aedeagal apodeme more or less triangular in profile, basally bifurcating at juncture with each lateral gonite.

Female Terminalia: Female ventral receptacle (Figure 45) with operculum as high as wide, broadly rounded, slightly flattened dorsally; extending process short, distinctly narrowed apically, shallowly curved. Segments 6 and 7 complete; sixth spiracle situated near anteroventral corner of sixth tergum; sixth sternum narrowly rectangular, about 3 times longer than wide, more setose posteriorly; seventh sternum narrowly rectangular, about two and one-half times longer than wide, more setose posteriorly. Eighth segment as follows: tergum divided into 2 lateral tergites, each gradually becoming wider ventrally; sternum divided longitudinally, each sternite about 3 times longer than wide, narrowed and more setose posteriorly, bearing 3-4 large

apical setae. Ninth sternum sclerotized basally, divided, with poorly sclerotized area posteriorly and lacking dividing sulcus, setose more toward base, each sternite with 1 large bristle, well developed; ninth tergites fused with cerci and each bearing 1 large bristle posteroventrally.

DESCRIPTION OF IMMATURE STAGES.—*Egg* (Figure 46): Length 0.75-0.90 mm (\bar{x} = 0.82); maximum width in dorsal view 0.25-0.36 mm (\bar{x} = 0.31). Ovoid; egg membranes transparent. Similar to *C. austrina* except in the following characters. Yellowish orange just after oviposition, becoming lighter yellow to dull white during development. Surface of chorion nodulose, without reticulate pattern. Micropyle in less distinct circular depression and surrounded by pale, flat, spinelike processes. Opposite end somewhat tapered posteroventrally. (Based on 27 specimens from rearings.)

First-Instar Larva: Main body length is 1.64-2.41 mm, respiratory tube length 0.31-0.47 mm; maximum width in dorsal view 0.31-0.33 mm. Similar to *C. austrina* except in the following characters. Posterior spiracular caps as in Figure 50 very similar. Cephalopharyngeal skeleton



FIGURES 46-56.—*Cirrula gigantea*: 46, egg, lateral aspect; 47, anterior spiracle of second-instar larva, lateral aspect; 48, same of third-instar larva, lateral aspect; 49, third-instar larva, anteroventral aspect; 50, posterior spiracular cap of first-instar larva, lateral aspect; 51, same of second-instar larva, median aspect; 52, same of third-instar larva, median aspect; 53, same, distal aspect; 54, cephalopharyngeal skeleton of second-instar larva, lateral aspect; 55, epistomal sclerite of third-instar larva, dorsal aspect; 56, cephalopharyngeal skeleton of third-instar larva, lateral aspect.

length 0.29–0.31 mm. (Based on 17 reared specimens.)

Second-Instar Larva: Main body length 3.50–5.53 mm, respiratory tube length 0.75–1.34 mm; maximum width in dorsal view 0.59–0.78 mm. Similar to *C. austrina* except in following characters. Anterior spiracles (Figure 47) very similar, with 5–6 marginal papillae. Prolegs lacking distinct glabrous borders anteriorly and posteriorly. Posterior spiracular caps (Figure 51) very similar. Cephalopharyngeal skeleton (Figure 54) length 0.51–0.54 mm; posterior arms of epistomal sclerite more slender and less diverging; lateral pharyngeal processes fused to pharyngeal sclerite. (Based on 26 specimens, 20 reared and 6 field collected.)

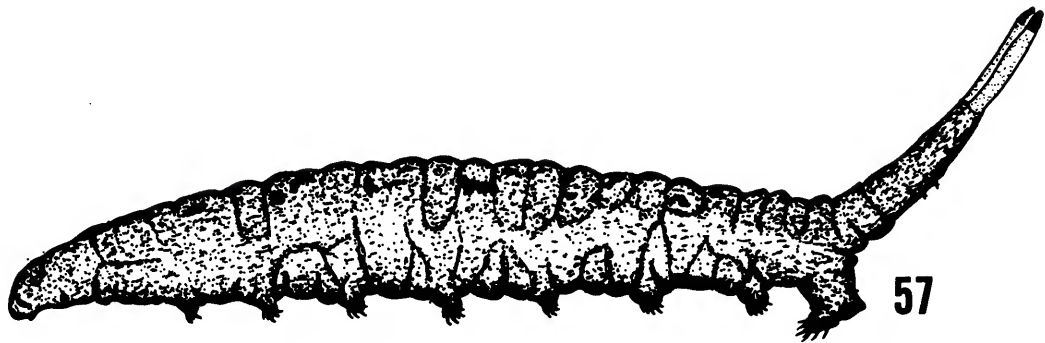
Third-Instar Larva (Figures 57, 58): Main body length 9.08–12.83 mm, respiratory tube length 2.89–4.83 mm; maximum width in dorsal view 1.66–2.83 mm. Similar to *C. austrina* except in following characters. Integument covering somewhat less dense, arcs of glabrous patches less evident. Antennae smaller. Anterior spiracles (Figure 48) very similar, usually with 6 marginal papillae. Transverse strap on segment 3 thicker and with a somewhat lighter perpendicular projection extending posteriorly (Figure 49). Venter of segments 3 and 4 more evenly spinose; distinct light areas absent. Posterior spiracular caps (Figures 52, 53) very similar; slightly larger. Cephalopharyngeal skeleton (Figure 56) length 0.92–0.98 mm. Mouthhook length 0.17–0.19 mm. Hypostomal sclerite length 0.28–0.32 mm. Posterior arms of epistomal sclerite more slender and less diverging (Figure 55). Pharyngeal sclerite length 0.42–0.50 mm, indentation index 67–75; lateral pharyngeal processes attached; dorsal cornua with more abundant dark rays. (Based on 19 specimens, 6 reared and 13 field collected.)

Puparium (Figures 59, 60): Main body length 7.07–9.33 mm (\bar{x} = 8.56), respiratory tube length 4.40–6.09 mm (\bar{x} = 5.27); maximum width in dorsal view 2.07–2.83 mm (\bar{x} = 2.53). Similar to *Cirrula austrina* except in the following characters. Transverse sclerotized strap on segment 3 with lighter posterior projection. Prolegs 6 and 7 moderately swollen and protruding; terminal proleg

(P₈) swollen and protruding, usually opposed to P₇. (Based on 33 specimens, 3 reared and 30 field collected.)

TYPE MATERIAL.—Holotype male of the senior synonym is labeled: “♂/Cohasset IX [Sep] 8 [19] 04 Mass[achusetts][date handwritten]/HOLOTYPE 6072 [number handwritten, red]/HOLOTYPE *Cirrula gigantea* ♂ E. T. Cresson Jr [name and sex symbol handwritten, red].” Three female paratypes have the same locality data as the holotype. The holotype is pinned directly, is in poor condition (the head is missing, both wings slightly torn), and is deposited in the Academy of Natural Sciences of Philadelphia, type number 6072. One of the female paratypes is labeled as an allotype, although none was designated in the original description. The holotype female of the junior synonym is labeled: “White Mount[ain] [New Hampshire] 879-I/Pogonephydra chalybea H. det. Hendel [name and initial handwritten]; Coll. Hendel.” The holotype is pinned directly, is in fair condition [the right wing is tattered, the left wing was removed and slide mounted], and is deposited in the Naturhistorisches Museum, Wien, Austria.

OTHER SPECIMENS EXAMINED.—CANADA. NEW BRUNSWICK: Kouchibouguac National Park, 8 May 1977, J. E. H. Martin, J. F. McAlpine (1♂, 1♀; CNC); Shippigan, 14 Jul 1931, J. M. Aldrich (16♂, 49♀; USNM). NOVA SCOTIA: Baddeck, 16 Jul 1936, T. N. Freeman (8♂, 10♀; CNC); Lockeport, 29 Jul–9 Aug 1958, J. R. Vockeroth (4♂, 4♀; CNC); Petite Riviera, 12–18 Jul 1935, J. McDunnough (2♀; CNC); Sable Island, 11–15 Sep 1967, W. R. M. Mason (1♀; CNC). PRINCE EDWARD ISLAND: Brackley Beach, Canadian National Park, 25–28 Jul 1940, J. McDunnough (1♂, 7♀; CNC); Green Gables, Cavendish Beach, 22 Jul 1967, D. M. Wood (1♀; CNC). QUEBEC: Alright Island, 17 Aug 1917, F. Johansen (3♂, 5♀; CNC); New Richmond, 6 Aug 1954, J. E. H. Martin (31♂, 39♀; CNC); Notre Dame du Portage, 17 Aug 1957, W. J. Brown, W. R. M. Mason (3♂, 1♀; CNC). UNITED STATES. CONNECTICUT: Fairfield Co., Stratford (1♀; USNM). New Haven Co., New Haven, W shore of harbor, 29 Jul 1961, D. L. Deonier (58♂, 52♀; DLD). MAINE: Hancock Co., Narrows, Mt. Desert, 13 Aug 1900, C. W. Johnson (1♂, 1♀; USNM). Sagadahoc Co., Popham Beach, 14 Jul 1971, P. Ward (1♀; CNC). Washington Co., Machias, 17 Aug 1909, C. W. Johnson (1♂, 1♀; USNM). MASSACHUSETTS: Barnstable Co., Cape Cod, 10 Sep, Scudder (1♂; USNM); Chatham, 30 Jun 1904, C. W.

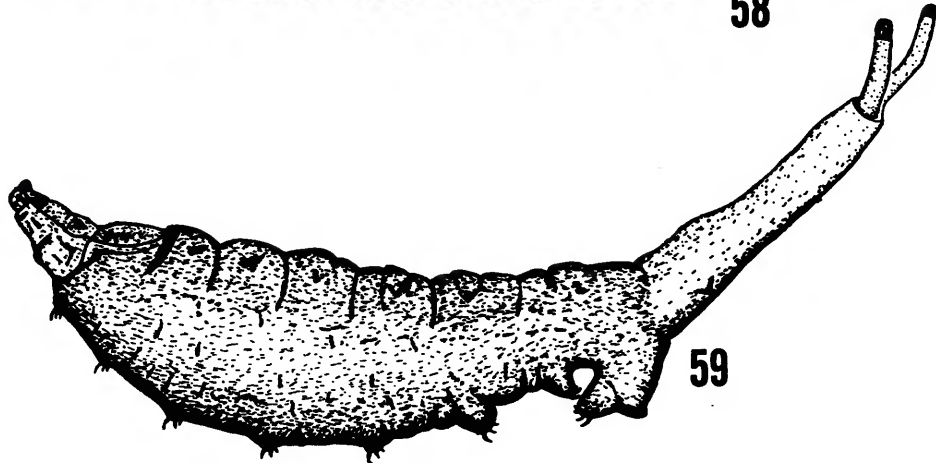


1.0

57

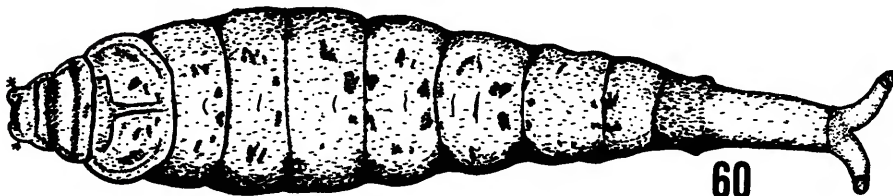


58



1.0

59



60

FIGURES 57-60.—*Cirrula gigantea*: 57, third-instar larva, lateral aspect; 58, same, dorsal aspect; 59, puparium, lateral aspect; 60, same, dorsal aspect.

Johnson (1♂; USNM); Eastham, 27 Jun 1904, C. W. Johnson (1♂; USNM); Falmouth Heights, 6 Aug 1918 (2♀; USNM); Provincetown, 18 Aug 1926, A. L. Melander (1♂; USNM); Woods Hole, 22 Jul–2 Aug 1899–1900 (3♂; AMNH, USNM). Dukes Co., Naushon Island (1♀; USNM). Essex Co., Gloucester, 24 Jun 1924, C. W. Johnson (2♀; CNC); Ipswich, 22 Jul 1961, W. W. Wirth (1♀; USNM); Nahant, 6 Jul 1919, C. C. Sperry (1♂, 3♀; USNM). Norfolk Co., Brookline, F. C. Bowditch (1♀; USNM); Cohasset, 8 Nov 1904, C. W. Johnson (2♀; USNM). Suffolk Co., Boston, vicinity of, 29 Jun 1908, W. E. Britton (1♀; USNM). NEW HAMPSHIRE: White Mountains (1♂, 1♀; AMNH, USNM; questionable, see "Remarks" section).

GEOGRAPHIC DISTRIBUTION (Figure 61).—*Cirrula gigantea* occurs along the coast of eastern North America from between 41° and 49° north latitude.

NATURAL HISTORY.—Field notes were recorded and laboratory rearing initiated with material from the following localities and dates. Connecticut: New Haven Co., Plum Bank Beach, 1 Jun

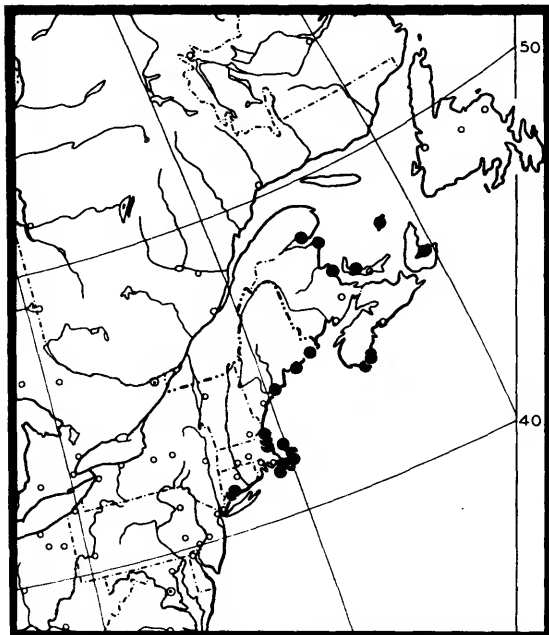


FIGURE 61—Distribution map of *Cirrula gigantea*.

1971, 6 Aug 1971. Massachusetts: Barnstable Co., Eastham, 25 May 1969, 4 Aug 1971. The earliest seasonal record for adults is 27 Mar (Massachusetts); the latest, 24 Sep (Massachusetts).

Adults were observed walking on salt marsh algae and mud, and were also taken by sweeping the marsh habitat. They were much less abundant than *Ephydra subopaca* Loew and *Dimecoenia spinosa*, two other species of Ephydrini occurring in the same marshes. Adults are strong fliers, commonly flying out of sight after being disturbed. No courtship or mating behavior were observed, although a male of an *Ephydra* species once mounted a female of *Cirrula gigantea* but was quickly dislodged.

Larvae and puparia were found infrequently during the months of July, August, and September. An algal mat approximately two feet in diameter at Plum Bank Beach yielded 38 puparia on 1 Jun 1971 (Figure 117). These puparia produced 29 adults of *C. gigantea* and one parasitoid wasp (Pteromalidae, *Belonura singularis* Ashm.); eight were inviable.

When confined in laboratory breeding containers, adults were comparatively awkward and clumsy. They often attempted to climb up the sides of the container, only to fall into the bottom. They also attempted to fly out, making a distinctly audible sound as they hit the sides and lid of the containers. Larger rearing chambers were constructed from 18 × 13 × 36 cm plastic boxes in an attempt to increase the flies' longevity. Each container was supplied with moist peat moss, three to five small petri dishes filled with salt marsh algae, and small clumps of grass. The flies, however, lived no longer than those confined in the smaller containers.

No eggs were found in nature, but females readily oviposited in the rearing containers, usually on or within the salt marsh algae, but also occasionally in the peat moss. Maximum recorded egg production was 252 eggs during a 14-day period; the maximum daily output was 47 eggs.

The incubation period was two days (66 observations). Newly hatched larvae usually fed readily on field-collected salt marsh algae. A few larvae initially crawled away from the algae, but later returned and commenced feeding. The feeding mechanism, as well as the overall appearance and behavior, is very similar to that of *C. austrina*.

The first stadium lasted two to three days (25 observations); the second, three to five days (21 observations); the third, five to eight days (18 observations). Larvae of all three instars were usually feeding when observed, at times being completely covered by the algae with the exception of the posterior spiracles. Puparia were formed just beneath the surface of the substrate, with the respiratory tube projecting slightly above. The pupal stage lasted eight to twelve days (17 observations).

REMARKS.—The locality data cited for the junior synonym, *Pogonephydra chalybea* Hendel, is undoubtedly incorrect. The species is only known from coastal marshes where it feeds on algae growing in such habitats. Consequently, we are of the opinion that this specimen was mislabeled.

Genus *Dimecoenia* Cresson

Dimecoenia Cresson, 1916:152 [type-species: *Coenia spinosa* Loew, by original designation].—Sturtevant and Wheeler, 1954:166 [review].—Wirth and Stone, 1956:472 [review, species of California].—Wirth, 1965:755 [catalog].—Steyskal, 1970:462–465 [review].

DIAGNOSIS.—Specimens of *Dimecoenia* may be distinguished from those of other genera of the tribe by the following combination of character states.

Adults: Cruciate intrafrontal bristles 1 pair, well developed; latero-clinate fronto-orbital bristles 2 pairs, slightly divergent; third antennal segment simple, lacking secondary bristle inserted laterally just below arista; arista tapering gradually from thickened base to stylelike apex, approximately basal two-thirds with dorsal rays, thereafter bare, arista rays nearly as long as width of second antennal segment; ventral mar-

gin of antennal depressions nearly horizontal, not sloping ventrally at conspicuous angle; posthumeral bristle lacking; dorsal costagial bristle subequal in size to anteroventral costagial bristle; costa with numerous, conspicuous, spinelike setae; legs of both sexes similar; aedeagus a simple tube or bifurcate; female ventral receptacle variously shaped.

Third-Instar Larva: Ventral prolegs and dorsal markings lacking; third segment lacking transverse sclerotized strap; spiracular openings each subdivided, spiracular caps elongate; larvae usually in mud or sand substrates.

DISCUSSION.—As characterized here, the concept of *Dimecoenia* now comprises but two species: *D. fuscifemur* Steyskal and *D. spinosa* (Loew). The monophyly of the genus is established by the following apotypic character states:

1. Setae of costa: most members of the tribe Ephydrini have distinct setae along the anterior margin of the costa, albeit weakly developed and inconspicuous. The anteroventral costal margin of both species of *Dimecoenia* have conspicuous spinelike setae (see Figures 111–114).

2. Conformation of the ventral margin of antennal fovea; in most members of Ephydrini, the ventral margin of the antennal fovea slopes ventrally at a distinct angle toward the posteroventral corner of the face. In specimens of both species of *Dimecoenia* this margin is rounded, nearly horizontal, and not steeply angled. We interpret this to be a unique, derived condition.

Larvae of *Dimecoenia* represent an apparent reversal in the generalized adaptive scheme of Ephydrini. Whereas the larvae of other genera inhabit algal mats near the water's surface, those of *Dimecoenia* inhabit mud substrates of salt marshes. The mud habitat is typical of most genera of Scatellini from which the Ephydrini evolved. Accompanying the habit reversal in the apparent atrophy of the prominent, ventral prolegs. Crochet bearing prolegs are functionally adapted to algal mats, but would hinder any movement in a mud substrate where streamlining would be more advantageous.

Key to Species of *Dimecoenia* Cresson

ADULTS

- Femora concolorous with mesopleuron, moderately densely pollinose, mostly bronzish green to bluish green, with some cinereous coloration; posterior crossvein nearly straight, not conspicuously arched inwardly; anterior fronto-orbital bristles latero-clinate to anterolatero-clinate; face between antennal bases mostly greenish blue, with cinereous pollinose vestiture and some bronzish coloration laterally and dorsally *D. fuscifemur* Steyskal
- Femora stramineous to yellowish, at most sparsely pollinose dorsally, grayish or greenish; posterior crossvein distinctly arched inwardly; anterior fronto-orbital oriented obliquely posterolaterad, almost parallel with posterior fronto-orbital; face between antennal bases with broad bronzish band *D. spinosa* (Loew)

THIRD-INSTAR LARVAE

- Each spiracular opening on posterior spiracular caps extremely elongate and with 9–12 light-colored oval areas (Figures 78, 92–93); anterior spiracles usually with 4 marginal papillae; widely distributed and common in maritime salt marshes *D. spinosa* (Loew)
- Each spiracular opening on posterior spiracular caps slightly elongate and subdivided into 2 elongate ovoid areas (Figure 101); anterior spiracles with 3 marginal papillae; rare *D. fuscifemur* Steyskal

Dimecoenia spinosa (Loew)

FIGURES 62–94, 114

Coenia spinosa Loew, 1864:99.*Caenia* [sic] *spinosa* [unjustified emendation].—Osten Sacken, 1878:204 [catalog].—Aldrich, 1905:631 [catalog].*Dimecoenia spinosa*.—Cresson, 1916:152.—Sturtevant and Wheeler, 1954:166 [review].—Wirth and Stone, 1956:472 [review].—Wirth, 1965:755 [catalog].—Steyskal, 1970:465 [review, figures of male and female terminalia].

Diagnosis.—Specimens of *D. spinosa* are similar to those of *D. fuscifemur* Steyskal but may be distinguished by the following combination of character states.

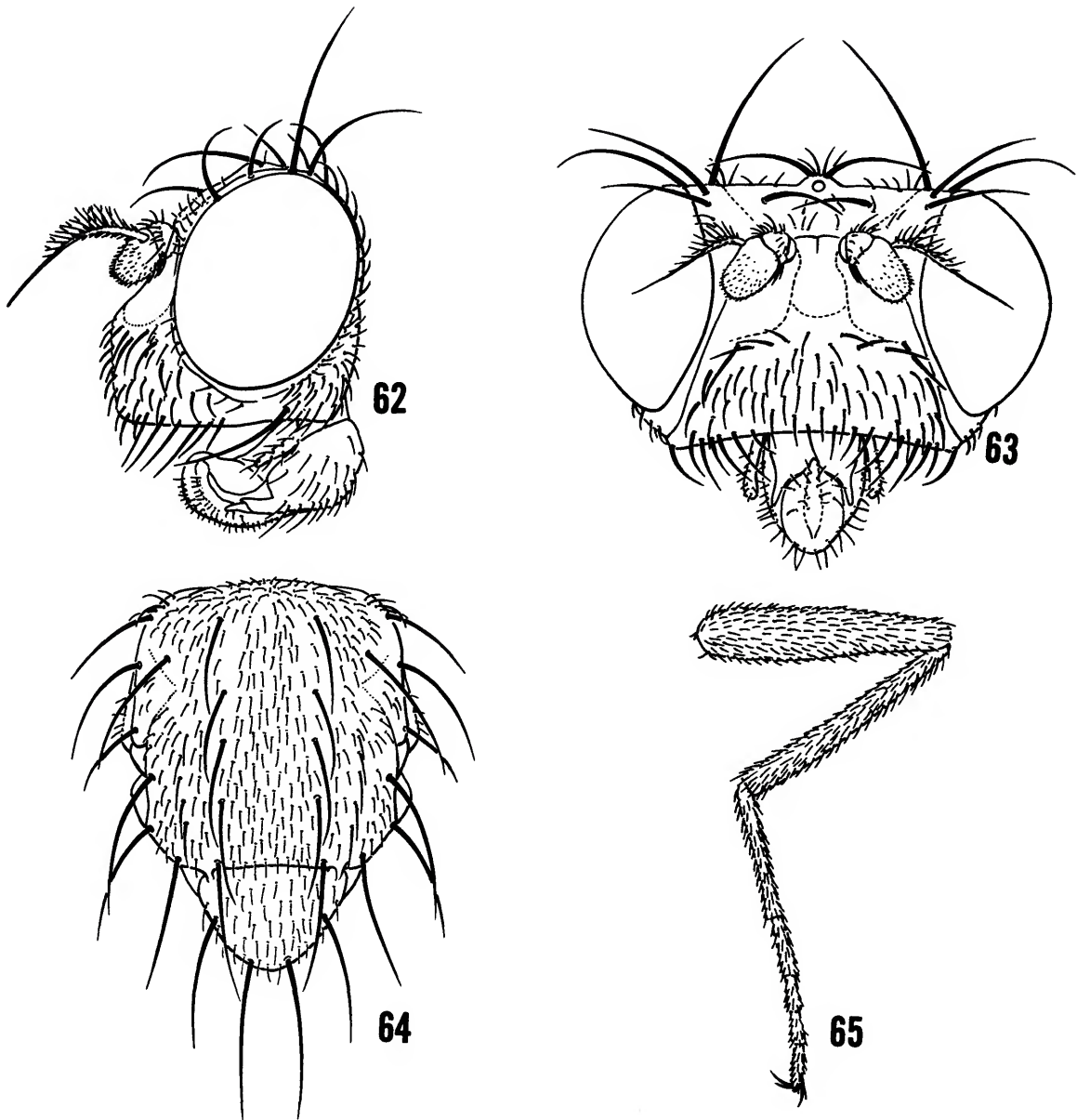
Adults: Latero-clinate fronto-orbital bristles nearly parallel to each other, only slightly divergent apically, both oriented obliquely at posterolateral angle; face between antennal bases with transverse band, yellowish brown to golden; coloration of thorax generally yellowish brown to brown, with considerable grayish overcast; legs, especially femora mostly stramineous to yellowish, at most with dorsum of femora grayish pol-

linose; costal spines of wing conspicuous, those of first costal section longer than one-half height of first costal cell; R stem vein lacking setulae above along posterior surface; posterior crossvein distinctly arched toward base of wing; aedeagus twice as long as wide; median surstylar process over two-thirds length of surstylus; apex of gonite deeply emarginate anteriorly; female ventral receptacle with operculum small, trapezoidal in shape, twice as wide basally as apically, extending process 3 times longer than width of operculum.

Third-Instar Larva: With 4 spiracular openings on posterior spiracular caps extremely elongate and subdivided into 9–12 oval areas each with 2 minute slits (Figures 92, 93); hydrofuge lamellae do not reach to end of the spiracular cap; anterior spiracles usually within 4 marginal papillae.

DESCRIPTION OF ADULT.—Moderately large to large shore flies, length 4.46 to 6.06 mm; mostly dull, olivaceous brown to grayish brown, dorsum with some subshiny to shiny areas.

Head (Figures 62, 63): Head width-to-length ratio averaging 1 : 0.57; frons width-to-length



FIGURES 62-65.—*Dimicoenia spinosa*: 62, head, lateral aspect; 63, same, anterior aspect; 64, thorax, dorsal aspect; 65, hind leg, lateral aspect.

ratio averaging 1 : 0.46; mesofrons with metallic bluish to greenish blue luster; parafrons not distinctly contrasting with mesofrons, subshiny; ocellar triangle more or less concolorous with

parafrons; ocelli arranged in equilateral triangle; median ocellus marking posterior margin of slight midline depression, not as well developed as in specimens of *C. austrina*; latero-clinate fronto-or-

bitar bristles nearly parallel, only slightly divergent apically; both bristles oriented at oblique angle posterolaterally; antenna mostly dark, but with pale, yellowish-orange areas, particularly toward posteroventral surface of third antennal segment; arista longer than combined length of first 3 antennal segments, subpectinate on basal two-thirds, rays greater than one-half width of second segment, apical third stylelike. Face width-to-height ratio averaging 1 : 0.85; dorsal slope of interfoveal carina barely evident, gradually projecting; dorsum and antennal fovea subshiny to shiny, mostly unicolorous and concolorous with shiny mesofrons; posterior margin of antennal fovea rounded along horizontal plane, not angling ventrally; lower portion of face gradually becoming lighter, nearly argenteous in color; facial setae uniform except along margins, marginal setae slightly larger, those extending from interfoveal carina widely separated in middle, numbering only 3-4 on each side; genal bristle large, prominent, much larger than any facial bristle. Eye width-to-height ratio averaging 1 : 1.25; eye-to-cheek ratio averaging 1 : 0.21. Gena moderately high; mostly bare and concolorous with face anteriorly, becoming darker and setose posteriorly; maxillary palp noticeably pale yellow, sometimes slightly pollinose, grayish.

Thorax (Figure 64): Generally dull, pollinose, mostly olivaceous brown to grayish brown; mesonotum at most subshiny and slightly darker than pleural areas, with vittate pattern of dark and light vittae, although difference between dark and light areas slight; posterior portion of mesonotum and scutellum darker, frequently subshiny, dark brown; acrostichal setae mostly uniseriated. Legs wholly tawny, femora at most pollinose dorsally, grayish to greenish or bluish gray; legs of both sexes similar, male without enlarged hind femur or explanate tarsomers bearing tufts of long hairs (Figure 65). Wing (Figure 114) length averaging 4.34 mm; wing length-to-width ratio averaging 1 : 0.48, costal vein index averaging 1 : 0.24; M_{1+2} vein index averaging 1 : 0.79, costal margin conspicuously spinose; R stem vein

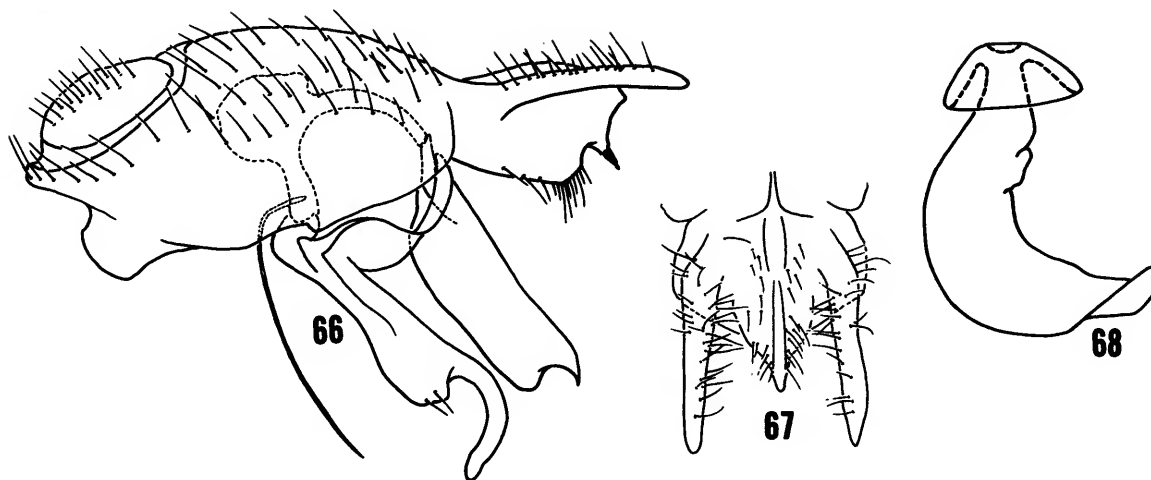
bare dorsally; sometimes with slight infuscation along crossveins and veins.

Abdomen: Generally subshiny; anterior portion of each tergum dark brown, posterior portion lighter, grayish green; male fifth tergum as long as wide, longer than fourth tergum.

Male Terminalia (Figures 66, 67): Epandrium more or less oval in caudal view, anteroventral margin evenly rounded; surstyli with large median flange and posterolateral, slender process; gonite 4 times longer than wide, anteroventral margin broadly and shallowly U-shaped; aedeagal apodeme with posteromedial broad wing; aedeagus a simple tube, mostly parallel sided.

Female Terminalia: Female ventral receptacle (Figure 68) with operculum much smaller than extending process, trapezoidal, extending process broadly curved, widest medially. Terga 6 and 7 complete; sixth tergum with spiracle situated toward posteroventral corner; sterna 6-7 whole; sixth sternum subrectangular, with anterior margin narrower, its length about one and one-half posterior width, with narrow, U-shaped median emargination anteriorly; seventh sternum rectangular, length about one and one-half width. Eighth segment as follows: 2 lateral tergites, well sclerotized, basal one-third enlarged, wider; sternum divided longitudinally, each sternite about 3 times longer than wide, posterior margin with 6-9 apical setae. Ninth sternum also divided, each sternite with large bristle at anterior margin; ninth tergites fused with ventral margin of cerci, each with large bristle at posteroventral margin generally more setose posteroventrally.

DESCRIPTION OF IMMATURE STAGES.—*Egg* (Figure 69): Length 0.68-0.72 mm (\bar{x} = 0.70); maximum width in dorsal view 0.24-0.28 mm (\bar{x} = 0.26). Creamy white just after oviposition; becoming whitish translucent after 12 hours; larval structures becoming visible through chorion after 36 hours. Ellipsoidal, somewhat flattened ventrally. Chorion surface lightly reticulate with irregular hexagonal pattern, becoming more irregular at micropylar end. Micropylar end bluntly rounded; micropyle slightly projecting from low, light brown swelling; no terminal depression. Pos-



FIGURES 66-68.—*Dimecoenia spinosa*: 66, male terminalia, lateral aspect; 67, ventral margin of epandrium and surstyli, posterior aspect; 68, female ventral receptacle, lateral aspect.

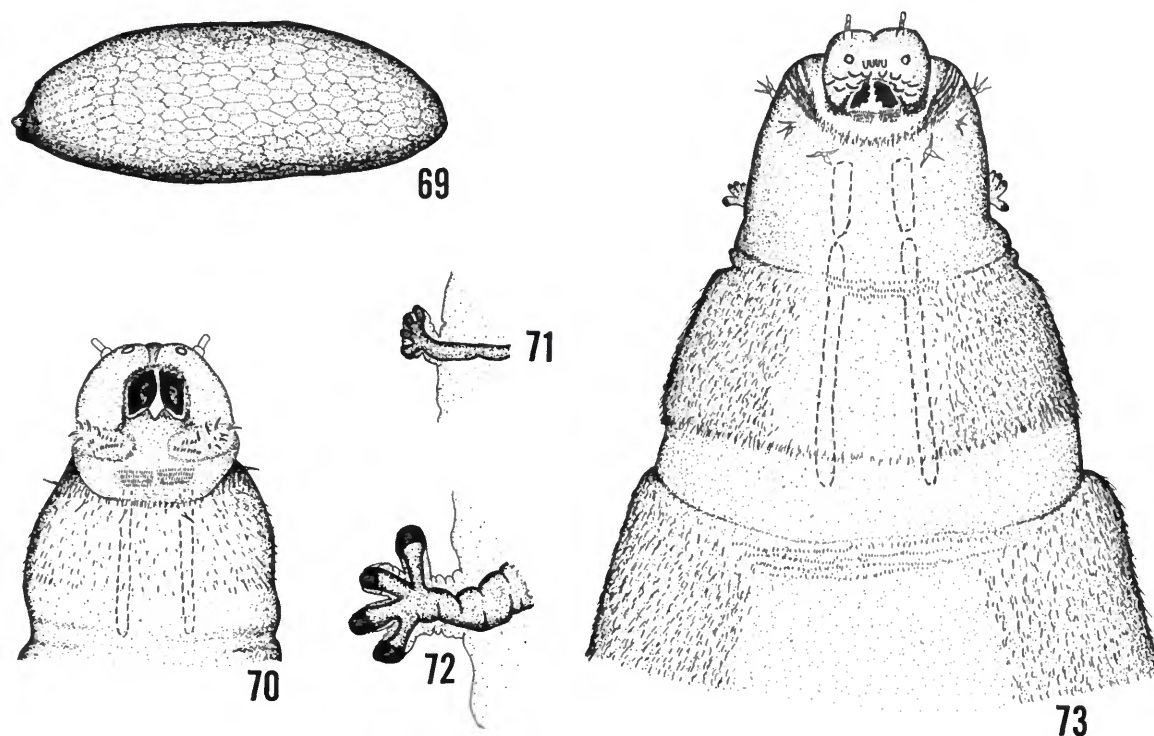
terior end somewhat abruptly tapered. (Based on 24 specimens from rearings.)

First-Instar Larva: Main body length 1.36–2.16 mm, respiratory tube length 0.36–0.64 mm; maximum width in dorsal view 0.24–0.40 mm. Similar to *C. austrina* except in the following characters. Oral spinules indistinct; lobes posterolateral to atrium more elongate transversely, spines much shorter (Figure 70). Prolegs vestigial or absent on segments 5–11. Segment 12 with subcylindrical proleg ventrally, without claws. Posterior spiracular caps (Figures 74, 76) much more elongate, with constriction between basal one-third and midlength. Cephalopharyngeal skeleton (Figures 79, 80) length 0.25–0.27 mm. Median edge of each mouthhook not tapering posteriorly but flattened and angled outward; dentate sclerite subtriangular. Posterior hypostomal bridge lightly pigmented, with lateral edges well separated from longitudinal rods. Height of sinus below dorsal cornua much less (compare Figures 20 and 79). (Based on 15 reared specimens.)

Second-Instar Larva: Main body length 1.96–4.48 mm, respiratory tube length 0.60–1.72 mm; maximum width in dorsal view 0.37–0.76 mm. Similar to *C. austrina* except in the following

characters. Prolegs vestigial or absent; sensilla less evident except on segments 11 and 12. First row of oral spinules much reduced. Postoral spine band more strongly developed laterally; dorsum of segment 2 noticeably darker; anterior spiracles (Figure 71) usually with 4 marginal papillae, rarely 3 or 5. Anterior two thirds of segment 3 banded by dense spinules except for 2 arcuate rows of small glabrous ovals; posterior one-third glabrous; sclerotized transverse strap absent on anteroventral margin of segment 3. Segment 4 densely spinose, interrupted by several small glabrous patches. Segments 5–11 darkly spinose; prolegs absent or vestigial. Basal portion of segment 12 with longer, darker spines than on remainder of body; subcylindrical, clawless proleg ventrally with no posterolateral spine patches. Respiratory tube with large, dark spines basally. Posterior spiracular caps (Figures 75, 77) much narrower basally, constricted near midlength. Cephalopharyngeal skeleton (Figure 81) length 0.45–0.50 mm. Mouthhooks not so strongly spoon shaped, tapering anteriorly. Epistomal sclerite darker, posterior portion lacking. (Based on 25 specimens, 13 reared and 8 field collected.)

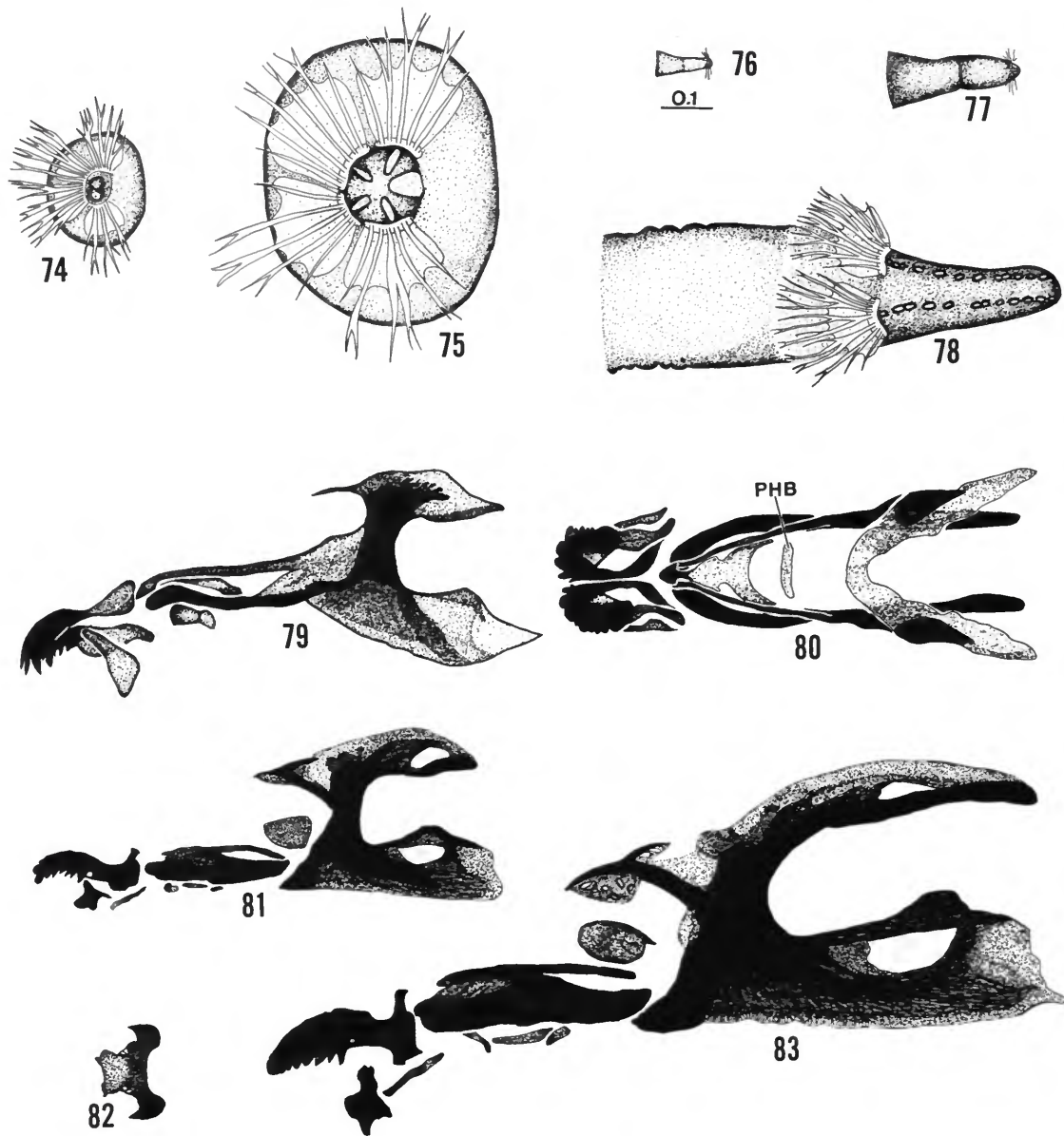
Third-Instar Larva (Figures 84, 85): Main body



FIGURES 69-73.—*Dimecoenia spinosa*: 69, egg, lateral aspect; 70, first-instar larva, anteroventral aspect; 71, anterior spiracle of second-instar larva, lateral aspect; 72, same of third-instar larva, lateral aspect; 73, third-instar larva, anteroventral aspect.

length 4.16–8.75 mm, respiratory tube length 1.16–2.83 mm; maximum width in dorsal view 0.75–1.50 mm. Similar to *C. austrina* except in the following characters: well-developed prolegs and dorsal patterns absent; integument covering generally darker, consisting of densely set hairlike spines (Figure 91); sensilla much less evident except on segment 12. Anterior row of 4 oral spinules much reduced, these papillae entirely pale (Figures 73, 89, 90). Segment 1 completely withdrawn in some specimens (Figure 88). Post-oral spine band better developed laterally, spines arranged in definite rows. Anterior spiracles (Figure 72) usually with 4 marginal papillae. Segments 4 and 5 and most of segment 3 densely spinose, with spines most dense dorsally; spines interrupted on these 3 segments by small, oval, glabrous patches, arranged in 2 arcs on each side

dorsolaterally; posterior one-fifth of segment 3 also glabrous. Segments 6–11 densely spinose, spines slightly darker dorsally; without dorsal patterns of flattened spines. Ventral prolegs reduced to small lobes; not armed with crochets but with slightly larger spines than remainder of integument, not arranged in definite rows. Basal portion of segment 12 set with long, dense spines. Large, subcylindrical proleg ventrally on segment 12; lacking crochets and posterolateral spine patches; perianal pad occupying most of ventral surface. Respiratory tube with long, dark spines basally; tapering and becoming sparsely spinulose near distal one-third; sensilla well developed. Posterior spiracular caps (Figures 78, 92, 93) elongate and pointed; spiracular openings greatly elongate and each subdivided into numerous small slitlike openings (Figures 92, 93), each pair



FIGURES 74-83.—*Dimecoenia spinosa*: 74, posterior spiracular cap of first-instar larva, posterior aspect; 75, same of second-instar larva, posterior aspect; 76, same of first-instar larva, lateral aspect; 77, same of second-instar larva, lateral aspect; 78, same of third-instar larva, lateral aspect; 79, cephalopharyngeal skeleton of first-instar larva, lateral aspect; 80, same, dorsal aspect; 81, same of second-instar larva, lateral aspect; 82, epistomal sclerite of third-instar larva, dorsal aspect; 83, cephalopharyngeal skeleton of third-instar larva, lateral aspect.

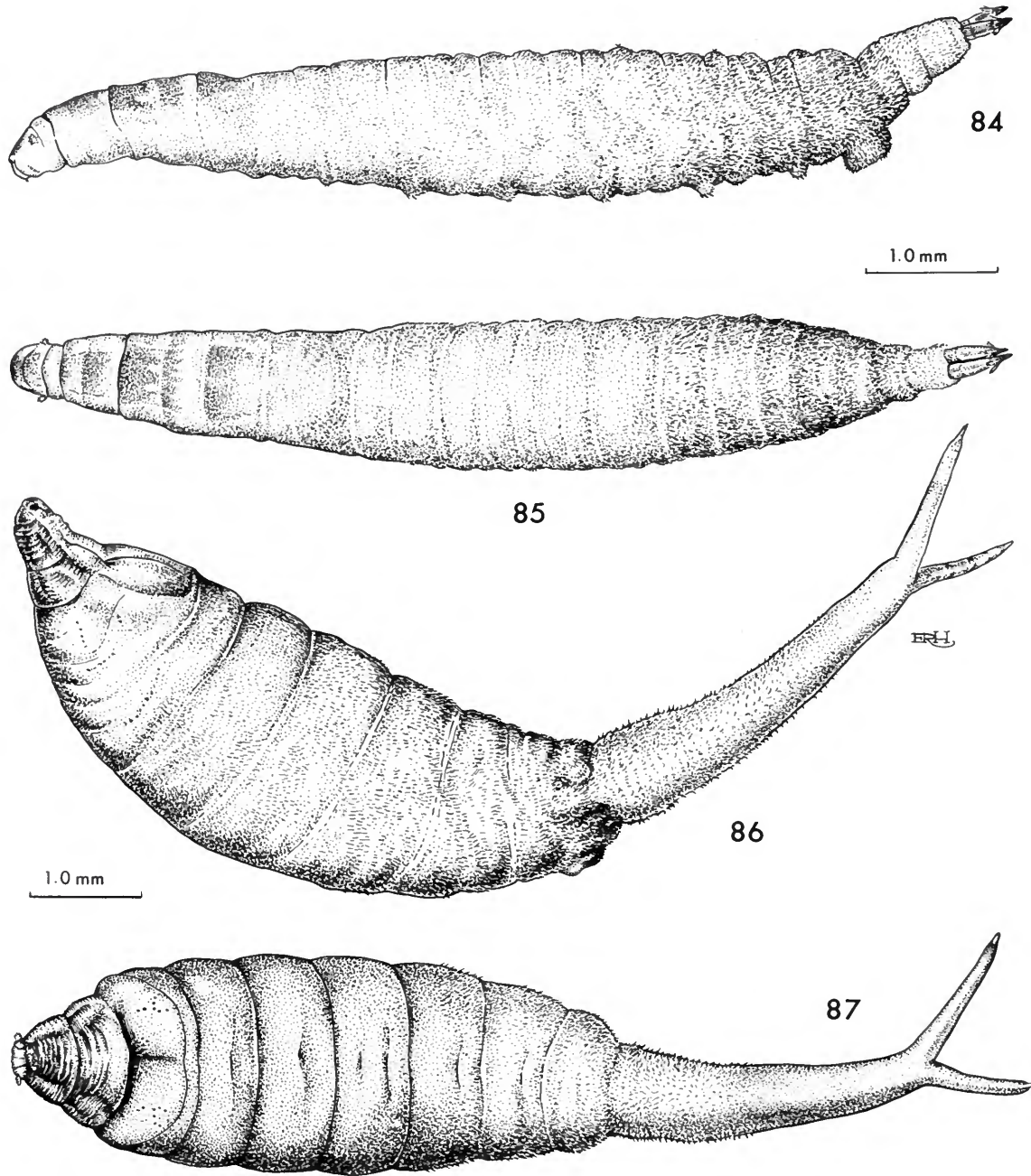
of openings located within a light-colored depression; hydrofuge lamellae well removed from and not reaching apex. Cephalopharyngeal skeleton (Figure 83) length 0.72–0.80 mm. Mouthhook length 0.15–0.16 mm; tapering anteriorly, not so strongly spoon shaped; small window at base of hook part. Hypostomal sclerite length 0.24–0.26 mm. Epistomal sclerite lacking posterior portion (compare Figures 24 and 82). Pharyngeal sclerite length 0.38–0.46 mm, indentation index 63–65; indentation nearly parallel sided horizontally (subcircular in *C. austrina*); ventral cornua stouter, its window smaller. (Based on 28 specimens, 7 reared and 21 field collected.)

Puparium (Figures 86, 87): Main body length 5.33–6.25 mm (\bar{x} = 5.88), respiratory tube length 2.92–5.33 mm (\bar{x} = 3.78); maximum width in dorsal view 2.00–2.17 mm (\bar{x} = 2.10). Similar to *C. austrina* except in the following characters. Transverse sclerotized strap absent from anteroventral margin of segment 3. Spines of integument covering darker and longer; no distinct dorsal patterns. Anterior spiracles usually with 4 marginal papillae. Each lateral 1/2 of dorsal cephalic cap more strongly convex at segment 5. Thin, moderately dark straps present anterodorsally on segments 6 and 7. Venter arcuate in lateral view from segments 5 to 11, lacking prolegs. Proleg of segment 12 weakly protruding; respiratory tube without tubercles, its position in relation to body highly variable (angle formed by respiratory tube and longitudinal axis of body 0°–90°). (Based on 33 specimens, 11 reared and 22 field collected.)

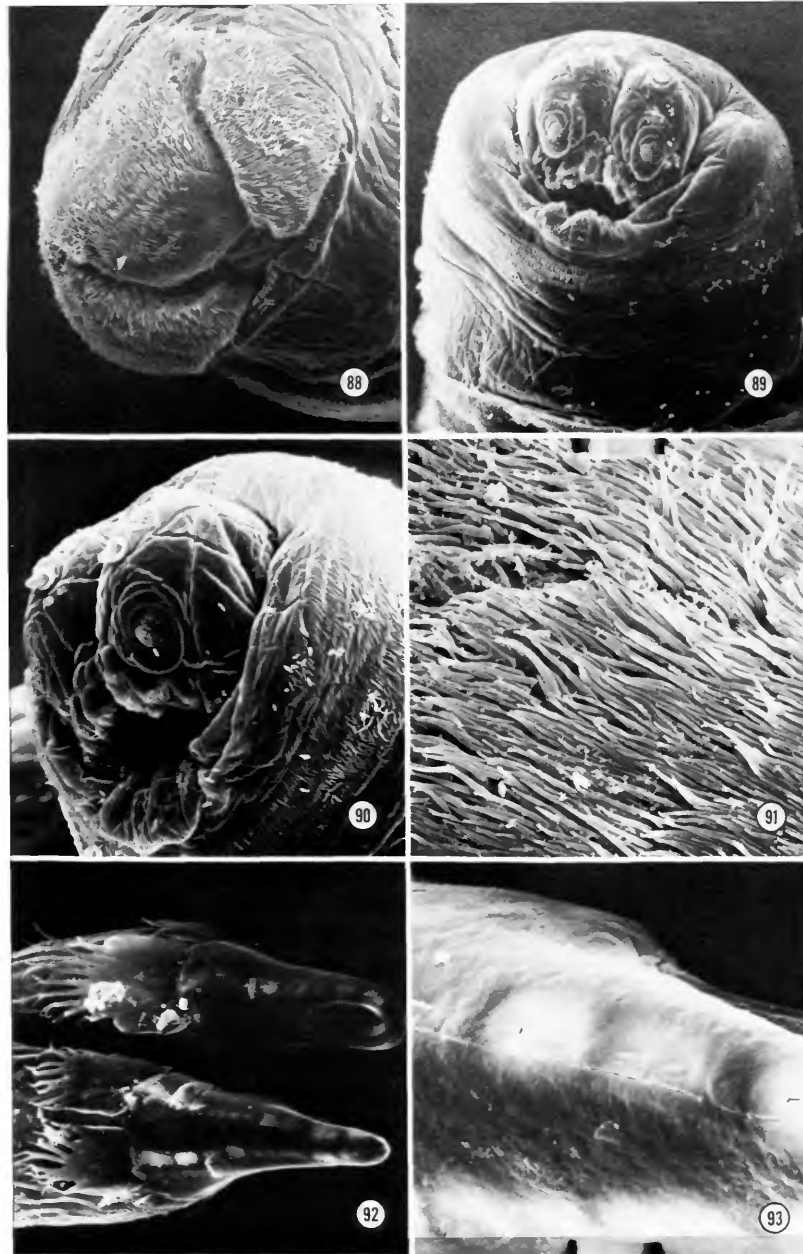
TYPE MATERIAL.—Lectotype female [here designated] is labeled: "Mass[achusetts]./123/Loew Coll./spinosa,m./Type 11182 [red]." The lectotype and the female paralectotype are mounted on the same pin; the bottom specimen is the lectotype. Both specimens are in the Museum of Comparative Zoology, Harvard University, MCZ type number 11182.

OTHER SPECIMENS EXAMINED.—CANADA. NEW BRUNSWICK: Birch Cove near Chamcook, 14 Aug 1957, G. E. Shewell (1♀; CNC); Tabusintac, 4 Aug 1939, J. McDunnough (1♀; CNC). NOVA SCOTIA: Lockeport, 29 Jul

1958, J. R. Vockeroth (1♂, 2♀; CNC). MEXICO. BAJA CALIFORNIA NORTE: San Quentin, 18 Jul 1922, G. D. Hanna (1♂; USNM). QUINTANA ROO: Espiritu Santo Bay, Cozumel, 5 Apr 1960, J. F. G. Clarke (1♀; USNM). JAMAICA. Falmouth, 1 Mar 1969, W. W. Wirth (1♂; USNM); Pt. Henderson, 24 Feb 1969, W. W. Wirth (1♀; USNM). UNITED STATES. CALIFORNIA: Orange Co., Corona del Mar, 15 Feb 1950 (2♀; USNM); Huntington Beach, 30 Jul 1932, R. H. Beamer (4♂, 2♀; KU); Santa Ana, 31 Mar 1961, J. Bath (13♂, 7♀; CU). San Diego Co., La Jolla, 13 Jul 1941, R. H. Beamer, B. Hogden (3♂, 1♀; KU, USNM); San Diego, 12 Mar 1897 (6♂, 2♀; AMNH, USNM); Sunset Beach, 12 June–30 Jul, 1935, 1948, R. H. Beamer, A. L. Melander (4♂, 4♀; KU, USNM). Ventura Co., Hueneme, 17 Jun 1948, W. W. Wirth (1♂, 1♀; USNM). CONNECTICUT: Fairfield Co., Westport, 13 Jul 1932, A. L. Melander (4♀; USNM). Middlesex Co., Old Saybrook (tidal marsh), 5 Sep 1968, K. R. Valley (2♀; CU); Plum Bank Beach, 0.8 mi SE Back River Bdge, 6 Aug 1971, K. W. Simpson (4♂, 3♀; CU); Westbrook, 22 Jul 1968, K. R. Valley (1♂, 2♀; CU); Westbrook, salt meadow nr Meadow Road and Clinton Road, 7 Jun 1970, K. W. Simpson (2♀; CU). DELAWARE: Kent Co., Bombay Hook National Wildlife Refuge, salt marsh, 9 Aug 1971, 3 Sep 1968, K. W. Simpson (5♂, 6♀; CU); Woodland Beach, salt marsh, 8 Sep 1968, K. W. Simpson (9♂, 12♀; CU). SUSSEX Co., Dewey Beach, 27 Aug–1 Sep 1972, L. Knutson (1♂, 1♀; USNM); Indian River Inlet, 45 m W US 14, 0.8 mi N, salt marsh, 12 Jul 1970, K. W. Simpson (7♂, 3♀; CU); Rehoboth, 25 Jun 1939, A. L. Melander (1♂, 4♀; USNM). FLORIDA: Broward Co., Hollywood, 1926 (1♀; KU). Dade Co., Biscayne Bay (1♀; AMNH); Everglades National Park, 10 Apr 1955, H. V. Weems (1♂; USNM). Collier Co., 22 Jan 1954 (1♂; USNM); Marco, 16 Dec 1925, W. E. Dove (1♂, 5♀; USNM); Seminole State Park, 17 May 1973, W. W. Wirth (1♀; USNM). Franklin Co., St. George Island, 5 Apr 1976, L. L. Pechuman (1♀; CU). Gulf Co., St. Joseph State Park, 1–3 May 1970, W. W. Wirth (2♂; USNM). Indian River Co., Sebastian, 9 Feb 1919, A. Wetmore (1♀; USNM). Lee Co., Fort Myers, 30 Mar 1912 (1♀; AMNH); Sanibel Island, 11 May 1973, W. W. Wirth (13♂, 8♀; USNM). Levy Co., Cedar Key, 12 Jul 1939, R. H. Beamer (3♂, 1♀; KU, USNM). Manatee Co., Oneco, 26 Apr 1955, J. C. Martin (1♀; CNC). Monroe Co., Cape Sable, 31 Mar 1953, W. R. M. Mason (4♀; CNC); Flamingo, Everglades National Park, 25 Jan 1939–7 May 1967, A. L. Melander, B. V. Peterson (9♂, 7♀; CNC, USNM); Key Largo, 2 May 1957–4 Apr 1966, H. V. Weems (2♂; CU, USNM); Plantation Key, 26 Feb 1956, R. A. Morse (1♂; USNM). St. John's Co., Crescent Beach, 0.65 mi W Mantanzas River, 3 Mar 1970 (1♂, 2♀; CU); Guana Wildlife Management Area, 15 Apr 1964, F. W. Mead (2♂, 2♀; CU); US Hwy A1A, 0.35 mi N St. Hwy 206, roadside ditch, 3 Mar 1971, K. W. Simpson (5♂, 2♀; CU). Volusia Co., Ormond (USNM). GEORGIA: (2♂, 10♀; USNM); S. Georgia, Morrison (1♂, 2♀; USNM). Glynn Co., Brunswick,



FIGURES 84-87.—*Dimecoenia spinosa*: 84, third-instar larva, lateral aspect; 85, same, dorsal aspect; 86, puparium, lateral aspect; 87, same, dorsal aspect.



FIGURES 88-93.—*Dimecoenia spinosa*: 88, third-instar larva, anteroventral aspect, invaginated; 89, same, anteroventral aspect, evaginated; 90, same, anterolateral aspect; 91, integumental covering on segment 3 of third-instar larva, dorsal aspect; 92, posterior spiracular caps of third-instar larva, dorsal aspect; 93, enlargement showing spiracular openings.

Torras Causeway, 0.55 mi W Back River, 2 Apr 1970. K. W. Simpson (1♂, 7♀; CU); Jekyll Island, 21 May 1974, L. Knutson (1♀; USNM); Jekyll Island, 0.2 mi W, 29 May 1969–27 Mar 1970, K. W. Simpson (11♂, 7♀; CU). LIBERTY Co., St. Catherine Island, 29 Oct 1977–21–23 Apr 1978, A. Hook, R. W. Matthew, (2♂; USNM). LOUISIANA: Tamany Par., Rigolets River, 6.5 mi W, US Hwy 90, 27 Mar 1971, K. W. Simpson (14♂, 38♀; CU). MAINE: Cumberland Co., Portland, 31 Jul 1950 (2♂; USNM). Hancock Co., Mt. Desert, Narrows, Jul–Aug 1927, C. W. Johnson (1♂, 1♀; USNM); Trenton, 1 Aug 1930, A. L. Melander (9♂, 6♀; USNM); Trenton, 2 mi S, 24 Jul 1968, K. Valley, R. Carde (2♂, 1♀; CU). MARYLAND: Calvert Co., Chesapeake Beach, 21 Apr–14 Oct, 1914–1930, J. M. Aldrich, R. C. Shannon (9♂, 18♀; USNM); Deale, 4 Sep 1977, L. Knutson (1♂, 3♀; USNM). MASSACHUSETTS: Barnstable Co., Cape Cod, N. Eastham, 18–22 Aug 1975, L. Knutson (3♂, 5♀; USNM); Cotuit, 10 Jun 1923 (1♀; USNM); Eastham, 3–6 Aug 1968–1971, K. W. Simpson, K. R. Valley (5♂, 16♀; CU); Falmouth, 13 Aug 1924 (1♀; USNM). N. Falmouth, 1–22 Aug 1922–1923 (2♀; USNM); Wellfleet, 29 Jun 1930, A. L. Melander (1♂; USNM); Woods Hole, 21 Jul–17 Nov, 1899–1922, A. H. Sturtevant (12♂, 18♀; AMNH, USNM). Bristol Co., Fall River, 3 Jul 1930, A. L. Melander (1♂, 2♀; USNM). Dukes Co., Martha's Vineyard, 19 Sep 1956, C. W. Sabrosky (2♂, 1♀; USNM); Naushon Island, 9–16 Jul–15 Aug, 1922–1926, A. L. Melander, A. H. Sturtevant (2♂, 5♀; USNM); Pasque Island, 15 Aug 1952 (2♂; USNM); Penikese Island, 7 Aug 1923 (2♀; USNM). Essex Co., Ipswich, 22 Jul–26 Jul, 1961–1973, L. L. Pechumen, W. W. Wirth (5♂, 4♀; CU, USNM); Lynn, 7 Aug 1914, H. M. Parshley (1♀; CU). Nantucket Co., Muskeget Island, 24 Nov 1915, W. L. McAtee (5♂, 4♀; USNM). Suffolk Co., Boston, Dec 1878 (1♂, 2♀; USNM). MISSISSIPPI: Hancock Co., Bay St. Louis, 4 mi W, 27 Mar 1971, K. R. Valley (2♂; CU). NEW HAMPSHIRE: Strafford Co., Durham, 12 Aug 1946, R. H. Beamer (3♂; KU). NEW JERSEY: Atlantic Co., Atlantic City, 2 Sep 1935, Blanton (1♂; CU). Cape May Co., Avalon, 8 Aug 1909 (2♀; USNM); Cape May, Jun 1904 (1♂; KU). Cumberland Co., Delaware Bay, 18 May–6 Oct 1936 (4♂, 19♀; USNM). Middlesex Co., Morgan, Jul 1925, Weiss and West (1♂; AMNH). Ocean Co., Great Bay Blvd., S. Tuckertown, 6 Jul 1973, R. F. Denno (1♂; USNM); Tuckertown, 1 Jul 1975, M. J. Raupp (1♂, 1♀; USNM). NEW YORK: Nassau Co., Long Beach, Long Island, 18 Aug 1952 (1♂; USNM). Queens Co., Rockaway, 10 Aug 1894, J. L. Zabrischic (2♀; AMNH). Richmond Co., Staten Island, South Beach, 7 Oct 1916 (2♂, 1♀; USNM). Suffolk Co., Babylon, Long Island, 30 May–9 Aug, 1933–1935, F. S. Blanton (6♂, 6♀; AMNH, CU); Cold Spring Harbor, Long Island, 27 Jun–6 Jul, 1921–1930, S. H. Emerson, A. L. Melander (12♂, 25♀; AMNH, USNM); Mt. Sinai, Long Island, 8 Sep 1935, Blanton (2♂, 2♀; CU). NORTH CAROLINA: Carteret Co., Beaufort, 28 Apr 1934, A. S. Pearse (1♂; USNM); Bogue Island, 7 May–17 Oct, 1974–

1975, G. C. Steyskal (9♂, 8♀; USNM). Dare Co., Nags Head, 15 May 1954, W. W. Wirth (3♂; USNM); Pea Island National Wildlife Refuge, 10 Oct 1972, N. H. Newton (1♂, 1♀; USNM). Onslow Co., Ashe Island, 6 Jul 1976, T. D. Edwards (1♀; USNM). TEXAS: Aransas Co., Aransas National Wildlife Refuge, 22 Apr–20 May, 1956–1972, W. W. Wirth (2♀; USNM). Galveston Co., Galveston, 2 Feb–5 Jun, 1900–1932, L. D. Tuthill (29♂, 17♀; AMNH, KU, USNM). Nueces Co., Corpus Christi, 1 Jan–12 Apr, 1906–1946, R. H. Beamer, F. C. Pratt (6♂, 9♀; KU, USNM). Willacy Co., Port Mansfield, 16 Aug 1970, D. Riley (1♀; DLD). VIRGINIA: Accomack Co., Assateague Island, 18 May–13 Aug, 1968–1971, K. W. Simpson, W. W. Wirth (12♂, 113♀; CU, USNM); Chincoteague Island, 25 Jun 1970, K. W. Simpson (4♂, 4♀; CU); Cockle Creek, 0.2 mi W, 9 Aug–20 Sep 1970, K. W. Simpson (8♂, 11♀; CU); Eel Creek Marsh, E of Chincoteague, 13 Aug 1971, K. W. Simpson (3♂, 2♀; CU).

GEOGRAPHIC DISTRIBUTION (Figure 94).—*Dimecoenia spinosa* is more widely distributed than *D. fuscifemur*. Wirth (1965) and Steyskal (1970) have recorded this species from both the Atlantic and Pacific coasts, as far north as New Brunswick in the East and San Francisco in the West. Its southern extensions reach Jamaica (Pt. Henderson) and Mexico (Cozumel, Espiritu Santo Bay; San Quintin, Baja California Norte).

NATURAL HISTORY.—Adults are often quite abundant in salt marshes, where they “skate” on the water's surface or walk on moist mud or algal substrates. At times they were observed resting on the stems or leaves of emergent vegetation, usually facing upwards. Adults occasionally were collected in freshwater areas that bordered salt marshes, but it was not determined if larval development was possible there.

Mating behavior was observed twice on 24 August 1971, along the St. Jones River, Kent Co., Delaware. The first observation began as a male and female fly approached one another on a moist mud substrate. The male quickly jumped over the female and landed with the tip of his abdomen almost touching the tip of the female's abdomen. He then turned around, followed her for a few inches, and mounted her after approximately 30 seconds. The female immediately spread her wings, curved her abdomen upwards, and allowed the male to copulate with her. After about 10 seconds, she dislodged him. The male

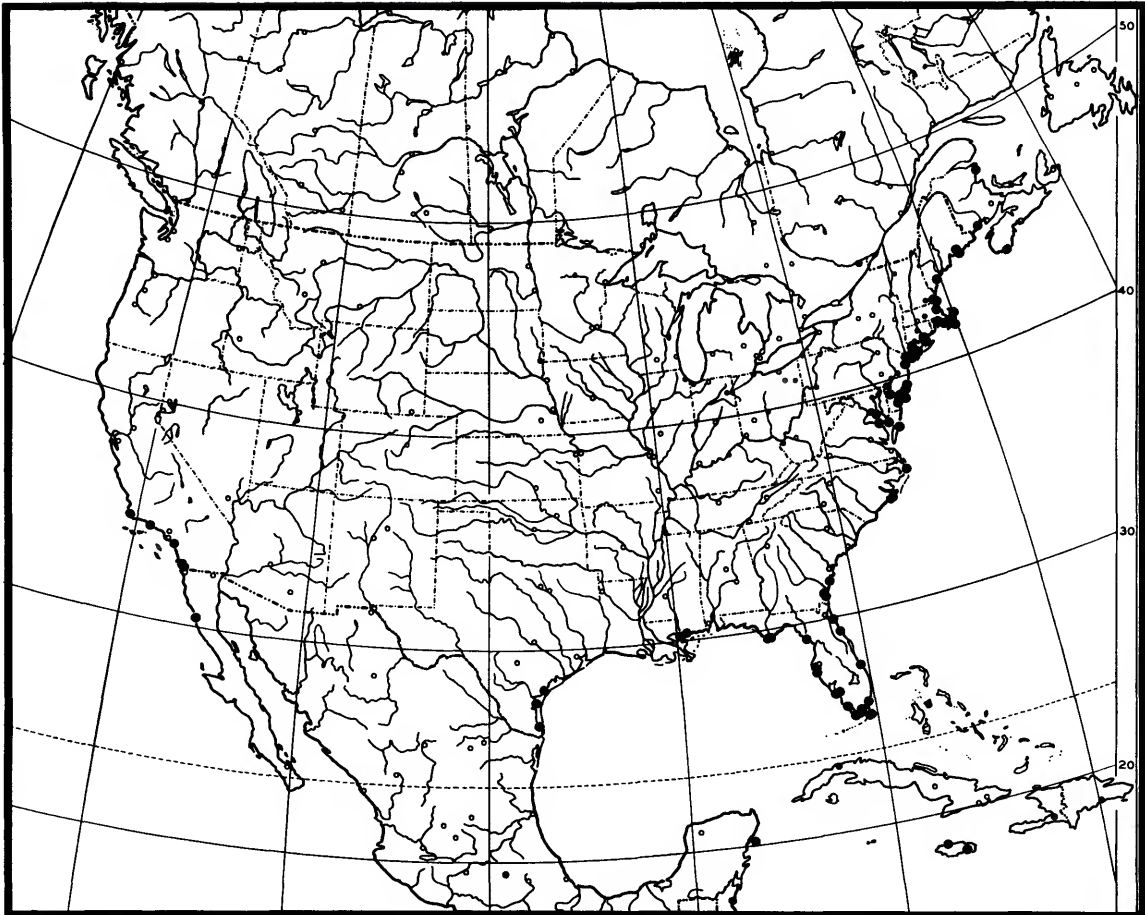


FIGURE 94.—Distribution map of *Dimecoenia spinosa*.

then extended his right wing at an angle of about 45° with his abdomen and held it completely still for 2–3 seconds. A second male displayed the same behavior after copulation had occurred.

Material to be reared was collected at the following localities and dates. Massachusetts: Barnstable Co., Eastham, 25 May 1969, 5 Aug 1971. Connecticut: Middlesex Co., Plum Bank Beach, 7 Jun 1970. Delaware: Sussex Co., Indian River Inlet, 12 Jun 1970. Virginia: Accomack Co., Chincoteague National Wildlife Refuge, 9 Aug 1970, 12 Aug 1971, Georgia: Glynn Co., Torreas Causeway, 1 mile east of Brunswick, 2 May 1970. Louisiana: St. Tammany Parish, U.S.

highway 90, 6.5 miles west of Rigolets River, 27 Mar 1971.

Adults maintained in the laboratory fed almost continuously on material within salt marsh algae and mud but also fed occasionally on the honey and brewers' yeast paste. Field-collected adult females of unknown age lived from 7–21 days; males from 6–12 days. Laboratory-reared flies were more difficult to maintain and usually died within five days after emergence. For this reason, premating and preoviposition periods were not determined.

Two third-instar larvae and seven puparia were collected from submerged detritus and mud col-

lected at St. Jones River in Kent Co., Delaware on 5 April 1970. This suggests that mature larvae and puparia are the overwintering stages for this species. Collecting and rearing records indicate that this species is multivoltine.

In breeding jars, eggs were sometimes laid in moist peat moss, but more commonly in the salt marsh algae or mud. They were deposited both on and just beneath the surface of the substrate, either singly or in clusters of up to 10 eggs. Eggs placed beneath the surface were located after the substrate was manipulated with a needle probe or a pair of forceps. Maximum recorded egg production was 226 eggs over a 7-day period; the maximum daily output was 59 eggs.

The incubation period ranged from 2–4 days under laboratory conditions, with 36 of 51 eggs hatching on the second day. Several hours before eclosion, each larva could be seen moving within the chorion and scraping the inside of the egg membranes with its mouthparts. This behavior continued periodically until the chorion was ruptured. Larvae enlarged the initial splits by pushing against the lateral and posterior portions of the chorion and were then able to eclose easily. Newly hatched larvae fed readily and developed most rapidly on a substrate of freshly collected salt marsh mud. Larvae of all instars grazed on this material, both submerging themselves within it and crawling on its surface, although submerision was more common. Duration of the first stadium ranged from 3 to 6 days (30 observations); the second, 4–6 days (18 observations); the third, 7–12 days (11 observations).

In laboratory colonies, puparia were formed just beneath the surface of the substrate, with at least part of the posterior respiratory tube projecting above the surface. Field-collected puparia were found by agitating the sand or mud bottoms of various salt marshes, then searching the surface for floating puparia. In several areas, the water depth was greater than 1 foot indicating that pupae can survive relatively far beneath the surface.

The gross morphology and microhabitat for the larvae of *D. spinosa* are unlike those of any

heretofore described species of Ephydrini. The larvae lack the well-developed ventral prolegs and dorsal spine patterns so characteristic of the tribe. Instead, the body is covered with the dense, hairlike spines and its overall appearance closely resembles ephydrid larvae in other tribes which live in muddy substrates such as *Parydra* Stenhammar (Deonier and Regensburg, 1978), *Coenia* Robineau-Desvoidy (Beyer, 1939) and *Ochthera* Latreille (Simpson, 1975). The larvae do, in fact, live in salt marsh mud. Several specimens were collected from mud substrates, and larvae reared in the laboratory preferred mud to algal mat substrates.

First- and second-instar larvae were less dependent on atmospheric oxygen than those of *C. austrina* or *C. gigantea*, and they remained completely submerged in mud substrates for extended periods of time. The posterior spiracles of these stages (Figures 74, 75) are nearly identical to those of *C. austrina* (Figures 14, 15) and *C. gigantea*. Either the larvae of *D. spinosa* have less of an oxygen requirement, or their cuticular respiration is much more efficient.

The posterior spiracles of the third-instar larva show a radical departure from the structure typical of Ephydrini. Each peritreme is greatly elongated and tapers to a point, and each spiracular opening has been subdivided into a series of small slits. These spiracles apparently function in obtaining oxygen from the roots of aquatic macrophytes. This rootpiercing adaptation has evolved several times in the Diptera, and is seen in other Ephydridae including *Notiphila* Fallén and *Hydrellia* Robineau-Desvoidy (Varley, 1937; Berg, 1950; Houlihan, 1969; Deonier, 1971; Busacca and Foote, 1978; Deonier, Mathis, and Regensburg, 1979).

The posterior spiracles have retained the hydrofuge processes, and in laboratory rearings, the spiracles were kept above the air-water interface by these structures. Therefore, in shallow waters, the larvae may utilize atmospheric oxygen. The hydrofuge processes, however, do not appear to be long enough to cover the spiracular openings when they are submerged. The extremely small,

slitlike openings probably serve to protect the tracheal system from being contaminated with water or dirt.

It is not known if all the instars can live deep within salt marsh mud and obtain enough oxygen for survival. The first- and second-instar larvae may be able to obtain enough oxygen via cuticular respiration due to their small size and high surface area to body weight ratio. The lower surface area to body weight ratio of the third-instar larva may have necessitated the development of the specialized root-piercing spiracles to augment cuticular respiration.

In an earlier paper, Simpson (1979) questioned whether this species represents a departure within the tribe Ephydrini, or whether it would lead to the placement of this species in another tribe of the Ephydrinae. Based on the similarities of the adults, and the similarities of larval characters such as the cephalopharyngeal skeleton, this species is recognized as a specialized form of the Tribe Ephydrini.

Dimecoenia fuscifemur Steyskal

FIGURES 95–110, 113, 118, 119

Dimecoenia fuscifemur Steyskal, 1970:463 [figures of male and female terminalia].

DIAGNOSIS.—Specimens of *D. fuscifemur* are similar to those of *D. spinosa* but may be distinguished by the following combination of character states.

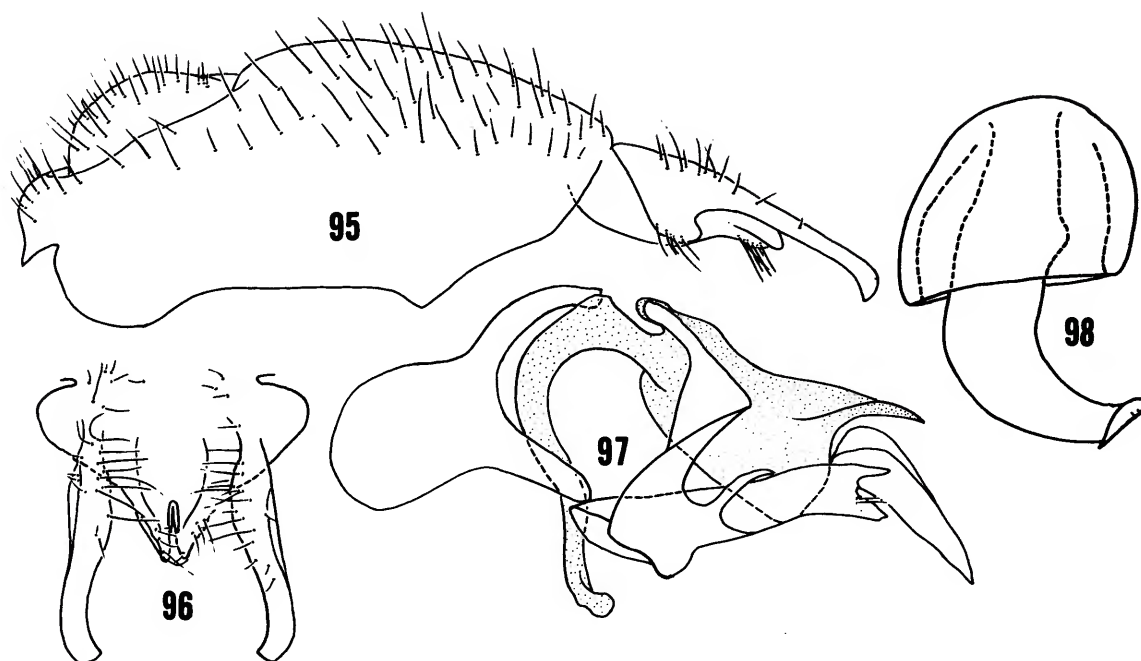
Adults: Laterocline fronto-orbital bristles divergent, anterior bristle oriented slightly anterolaterally, posterior bristle oriented laterally or slightly posterolaterally; face between antennal bases usually dark colored, with some bronzy coloration, rarely with conspicuous yellowish brown to golden transverse band; coloration of thorax generally brown to grayish brown but with considerable bluish to bluish green tinges, sometimes strongly so; femora mostly grayish to bluish or greenish gray, apically becoming yellowish, otherwise mostly stramineous; costal spines of wing evident but not as conspicuous as *D. spinosa*, shorter than one-half height of first costal cell;

stem R vein with 2–3 setulae above along posterior surface; posterior crossvein nearly straight, only very shallowly arched toward base of wing; aedeagus bifurcate, anterior lobe a slender, very gradually tapering process that is broadly bifid apically, posterior lobe nearly as wide apically as long; median surstylar process about one-half length of surstylus; apex of gonite nearly straight, very shallowly emarginate; female ventral receptacle with large operculum, lateral margins rounded, extending process only slightly longer than width of operculum.

Third-Instar Larva: With 4 spiracular openings on posterior spiracular caps slightly elongate and subdivided into 2 elongate ovoid areas; hydrofuge lamellae of posterior spiracles reach to end of spiracular cap; anterior spiracles with 2–3 marginal papillae.

DESCRIPTION OF ADULT.—Moderately large to large shore flies, length 4.24 to 5.37 mm; mostly dull but with considerable subshiny or shiny areas dorsally, grayish brown to mostly lightly bluish or greenish gray.

Head: Head width-to-height ratio averaging 1 : 0.63; frons width-to-length ratio averaging 1 : 0.66; mesofrons with metallic bluish green to deep greenish blue luster; parafrons contrasting distinctly with mesofrons, dull, dorsally pollinose, dark bluish gray with some to considerable bronzy coloration; ocellar triangle darker than parafrons but equally pollinose; ocelli arranged in equilateral or isosceles triangle, if the latter, posterior ocelli closer to one another than to median ocellus; median ocellus marking posterior margin of shallow midline depression, depression becoming shallower anteriorly; laterocline fronto-orbital bristles slightly divergent, anterior bristle slightly anterolaterocline, posterior bristle laterocline or but slightly posterolaterocline; antenna mostly unicolorous, blackish with dense pollinose vestiture, grayish to faintly greenish gray, dull; arista longer than combined length of first 3 segments, pectinate dorsally along basal two-thirds to three-fourths, longer rays nearly equaling width of second segment. Face width-to-height ratio 1 : 0.88; dorsal slope of interfoveal

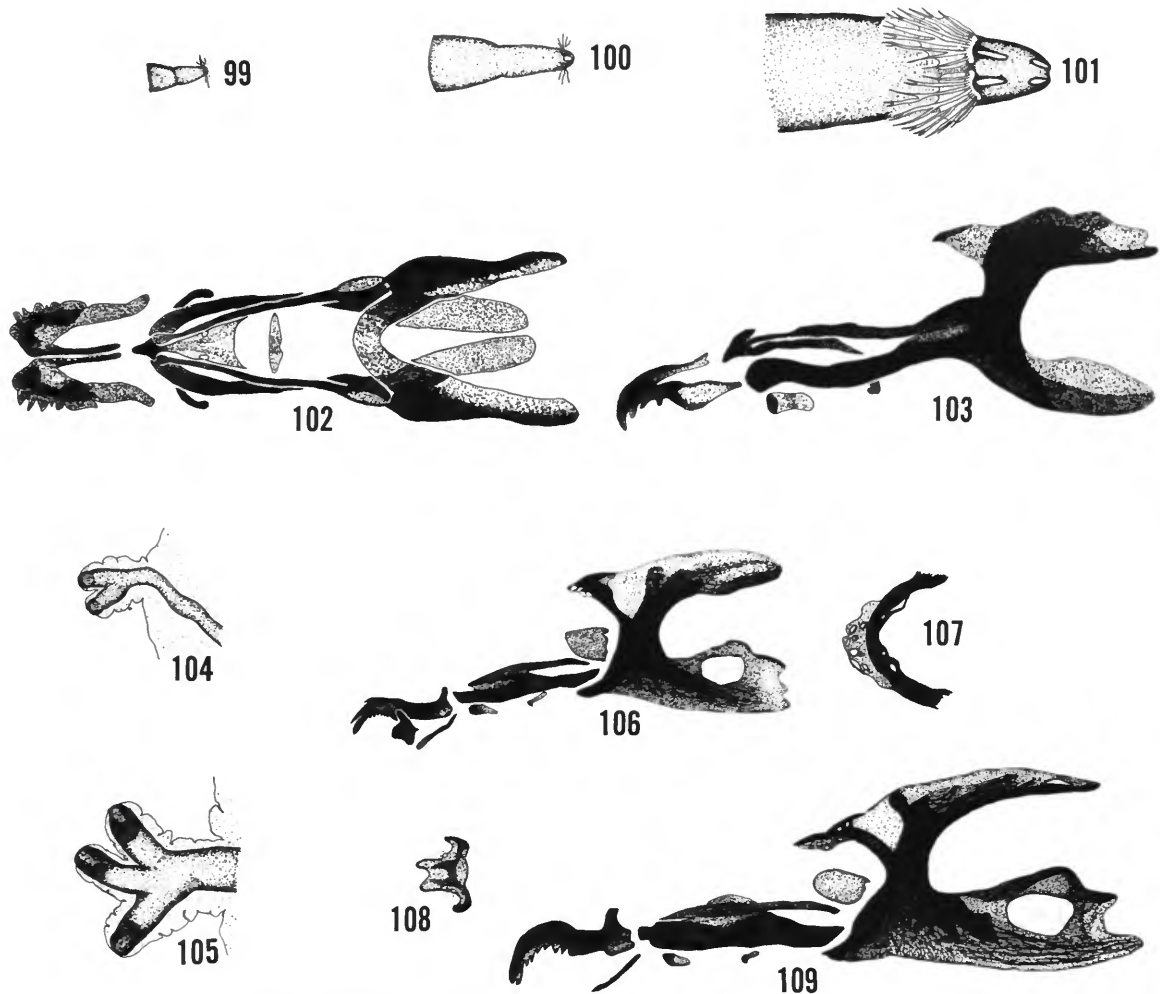


FIGURES 95-98.—*Dimecoenia fuscifemur*: 95, cercus, epandrium, and surstylus, lateral aspect; 96, ventral margin of epandrium and surstyli, posterior aspect; 97, internal male genitalia, lateral aspect; 98, female ventral receptacle, lateral aspect.

carina not projecting sharply, dorsum of carina concolorous with mesofrons but slightly more pollinose; antennal fovea distinct but not deeply depressed, mostly pollinose, becoming subshiny posterolaterally, ventral margin rounded along nearly horizontal angle, not sloping ventrally; facial area between antennal bases mostly bluish to slightly greenish gray, some specimens with some bronzy coloration but latter coloration not forming broad band between bases; facial prominence mostly gray to whitish gray, darker dorsally with some light bluish to greenish tinges; marginal facial setae distinctly larger than along oral margin, these angling inward, especially toward midline; other facial setae uniform in size and distribution. Eye prominent, nearly round, slightly higher than wide, eye width-to-height ratio averaging 1 : 1.3; gena moderately short, eye-to-cheek ratio averaging 1 : 0.16, mostly bare and concolorous with face, becoming more setose

and gradually darker posteriorly, with some faint greenish tinges; maxillary palp mostly stramineous brownish apically.

Thorax: Mesonotum dull to subshiny, lacking vittae, olivaceous gray anteriorly, dark brownish black to brownish dark blue posteriorly; scutellum concolorous with posterior portion of scutum; pleural areas gradually becoming lighter, more whitish gray anterior ventrally; mesopleuron olivaceous brown posterodorsally, becoming olivaceous gray anteroventrally; pteropleuron concolorous with posterior portion of mesopleuron but duller, more densely pollinose; sternopleuron olivaceous gray posteriorly to whitish gray anteriorly. Legs, except as noted, concolorous and not sexually dimorphic in size; femora mostly concolorous with propleuron, olivaceous gray, apices stramineous; tibiae and tarsi yellowish; front basitarsus of male with dark median annulus. Wing (Figure 113) length averaging 4.2 mm; wing



FIGURES 99-109.—*Dimecoenia fuscifemur*: 99, posterior spiracular cap of first-instar larva, lateral aspect; 100, same of second-instar larva, median aspect; 101, same of third-instar larva, lateral aspect; 102, cephalopharyngeal skeleton of first-instar larva, dorsal aspect; 103, same, lateral aspect; 104, anterior spiracle of second-instar larva, lateral aspect; 105, same of third-instar larva, lateral aspect; 106, cephalopharyngeal skeleton of second-instar larva, lateral aspect; 107, dorsal bridge of third-instar larva, dorsal aspect; 108, epistomal sclerite of third-instar larva, dorsal aspect; 109, cephalopharyngeal skeleton of third-instar larva, lateral aspect.

length-to-width ratio averaging 1 : 0.46; costal vein index averaging 1 : 0.26; M vein index averaging 1 : 0.85; costal margin with spines but not as well developed as in specimens of *D. spinosa*; R stem vein with 2-3 setulae above along posterior surface.

Abdomen: Segments concolorous, mostly faintly olivaceous greenish blue, darker, more bronzy or brownish basally, some specimens with considerable pollinose vestiture, dull, but usually sparsely so, subshiny; fifth tergum of male as long as basal width.

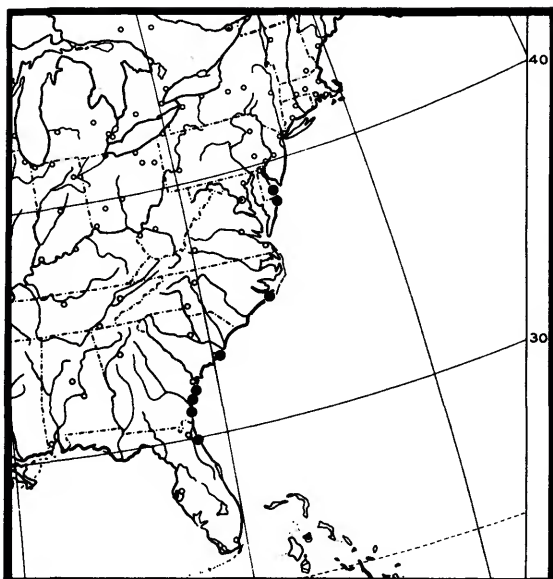


FIGURE 110.—Distribution map of *Dimecoenia fuscifemur*.

Male Terminalia (Figures 95–97): Epandrium somewhat parallel sided, slightly wider toward middle, poorly sclerotized medially, lateral margins also less sclerotized, rounded enlargement basally, with distinct angulation at point of attachment with internal genitalia; surstyli digitiform, more or less parallel sided, sinuate in caudal view and corniform medioapically, basomedial projection about one-half length of surstyli, cordate, bifid apically; aedeagus bifurcate, anterior lobe a slender tubelike process, broadly bifid apically, posterior lobe subrectangular, anterior margin rounded, posteroventral corner narrowly pointed; aedeagal apodeme with broad, rounded, dorsal wing; gonite with median shoulder, pointed apically.

Female Terminalia: Female ventral receptacle (Figure 98) with operculum about as high as wide, broadly rounded, extending process narrower apically, shallowly curved. Terga 6 and 7 complete; sixth tergum about twice as long as wide, anterior margin slightly wider than poste-

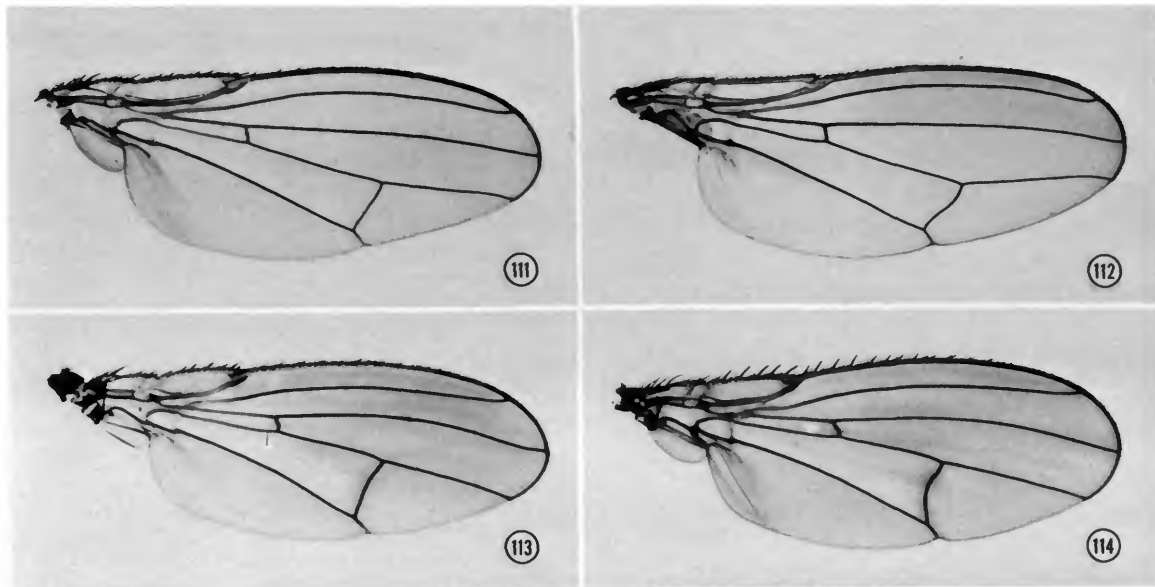
rior margin; seventh sternum subtrapezoidal, anterior width nearly double posterior width, anterior margin flat, posterior margin bluntly rounded. Eighth segment as follows: tergum incomplete, 2 lateral tergites, each becoming wider basally; sternum divided longitudinally, forming 2 bands, each about 3 times longer than wide and with more setae on posterior half, 3–4 apical setae. Ninth sternum also divided into 2 obclavate sternites each with anterior margin bearing 1 bristle, well developed; ninth tergite separated posteriorly from cercus by transverse sulcus, fused anteriorly, with more setae posteroventrally and with 1 bristle at posteroventral margin very well developed; cercus a broad winglike process, fused anteriorly with ninth tergite, setose posteriorly.

DESCRIPTION OF IMMATURE STAGES.—*Egg*: Length 0.76–0.84 mm (\bar{x} = 0.80); maximum width in dorsal view 0.26–0.32 mm (\bar{x} = 0.30). Similar to *D. spinosa* except posterior end less tapered. (Based on 16 specimens from rearings.)

First-Instar Larva: Main body length 1.32–2.01 mm, respiratory tube length 0.23–0.44 mm; maximum width in dorsal view 0.32–0.40 mm. Similar to *D. spinosa* except in the following characters. Lobes posterolateral to atrium armed with slightly longer and better-developed spines. Sensilla indistinct. Posterior spiracular caps (Figure 99) very similar. Cephalopharyngeal skeleton length 0.24–0.26 mm (Figures 102, 103). Dentate sclerite absent; median edge of each mouthhook tapering posteriorly. (Based on 10 reared specimens.)

Second-Instar Larva: Main body length 2.21–4.25 mm, respiratory tube length 0.50–1.40 mm; maximum width in dorsal view 0.45–0.85 mm. Similar to *D. spinosa* except for the following characters. First row of oral spinules absent. Postoral spine band weak, spines similar to those on remainder of integument. Anterior spiracles (Figure 104) with 2–3 marginal papillae. Posterior spiracular caps (Figure 100) very similar. Cephalopharyngeal skeleton (Figure 106) length 0.43–0.45 mm. (Based on 3 reared specimens.)

Third-Instar Larva: Main body length 4.33–



FIGURES 111-114.—Wings: 111, *Cirrula austrina*; 112, *C. gigantea*; 113, *Dimecoenia fuscifemur*; 114, *D. spinosa*.

5.83 mm, respiratory tube length 1.58–2.16 mm; maximum width in dorsal view 0.83–1.00 mm. Similar to *D. spinosa* except in the following characters. Anterior row of oral spinules absent. Postoral spine band much reduced, spines lightly pigmented and small. Sensilla present but much reduced. Anterior spiracles (Figure 105) with 2–3 marginal papillae. Small vestiges of ventral prolegs present on segments 5–12, these armed with small but distinct crochets. Posterior spiracular caps (Figure 101) shorter; each spiracular opening divided into 2 moderately elongate structures; hydrofuge lamellae reaching apex. Cephalopharyngeal skeleton (Figures 107–109) length 0.55–0.60 mm. Mouthhook length 0.13–0.15 mm. Hypostomal sclerite length 0.21–0.22 mm. Pharyngeal sclerite length 0.31–0.33 mm; indentation index 58–66. (Based on 3 reared specimens.)

Puparium: No material available.

TYPE MATERIAL.—Holotype male is labeled: "VIRGINIA [Accomack Co., salt marsh near southern end of Chincoteague National Wild-

life Refuge Assateague I[slan]d. 24 June 1967 Geo[rge]. Steyskal/HOLOTYPE DIMECOENIA FUSCIFEMUR Steyskal [name handwritten, pink with red subborder]." Allotype female and seven female paratypes are labeled with the same locality data as the holotype. Other paratypes are as follows. Virginia: Accomack Co., Revels Island (37° 31'N, 75° 40'W), 13 Oct 1915, W. L. McAtee (1♂; USNM). Georgia: McIntosh Co., Sapelo Island, 10 Sep 1963, Odum (1♂; USNM). The holotype is double mounted (minute nadel mounted in plastic base), is in fairly good condition (several bristles of the head are missing), and is in the National Museum of Natural History, Smithsonian Institution, USNM type number 70704.

OTHER SPECIMENS EXAMINED.—UNITED STATES. DELAWARE: Sussex Co., Dewey Beach, 27 Aug-1 Sep 1972, L. Knutson (1♂, 1♀; USNM). FLORIDA: John's Co., Crescent Beach, 0.65 mi W Mantanzas River, Route 206, 31 Mar 1971, K. W. Simpson (1♂; CU). GEORGIA: Glynn Co., 0.2 mi E Jekyll Island, Route 50, 27 Mar, 1970, 1 Apr 1971, K. W. Simpson (21♂, 12♀; CU, USNM); Liberty Co.,



FIGURES 115-119.—Larval habitats: 115, *Cirrula austrina*; 116, same, close-up; 117, *C. gigantea*; 118, *Dimicoenia fuscifemur*; 119, same, close-up.

St. Catherine's Island, 21 Apr-9 Oct 1978, J. W. Krispin and R. W. Matthews (8♂, 9♀; USNM). NORTH CAROLINA: Carteret Co., Bogue Island (inlet), 17 Oct 1974, G. Steyskal (1♂, 2♀; USNM). SOUTH CAROLINA: Charleston Co., Isle of Palms, 29 Mar 1969, K. W. Simpson (1♂; CU).

GEOGRAPHIC DISTRIBUTION (Figure 110).—*Dimecoenia fuscifemur* occurs along the eastern coast of the United States from Delaware south to Florida.

NATURAL HISTORY.—The longest series of specimens was collected near Jekyll Island, Glynn Co., Georgia, on 1 Apr 1970. The area was a fairly dry saltmarsh mud flat that was well removed from any standing water (Figures 118, 119). *Dimecoenia fuscifemur* seemed to be the only species of *Dimecoenia* in the area, and adults were concentrated in the open mud flat as opposed to the surrounding grasses. Shortly after the second author walked across the mud flat, adults congregated on the freshly exposed mud within his footprints.

Six pairs of adult flies from Jekyll Island were used to initiate laboratory rearings. The flies fed on the field-collected mud which was placed in

the containers. Field-collected males (7) lived from 7 to 21 days in laboratory colonies; females (6), 12 to 48 days. One female deposited 20 eggs over a 12-day period; the only other ovipositing female produced 36 eggs in four days.

The incubation period ranged from two to four days in the laboratory (19 observations). Newly hatched larvae crawled into mud which had been collected at Jekyll Island, fed, and molted to second-instar larvae after four days. At this time they apparently found the mud unacceptable and crawled onto the sides and the lids of the rearing containers. Saltmarsh algae and mud from other habitats were offered to the larvae in an attempt to find a suitable food source. However, 15 of the 19 larvae died as second-instars. The four survivors spent seven to eight days in the second stadium. Unfortunately, none of these larvae pupated; all died within eight days after molting to third-instar larvae. The rearing results may suggest that the larvae need a particular kind of algae. *Parydra* larvae will also feed on field-collected mud for a few days but then die unless diatoms are added (B. A. Foote, pers. comm.).

Literature Cited

- Aldrich, J. M.
 1905. A Catalogue of North American Diptera. *Smithsonian Miscellaneous Collections*, 46:1-680.
 1912. The Biology of Some Western Species of the Dipterous Genus *Ephydra*. *Journal of the New York Entomological Society*, 20(2):77-99, 3 plates.
- Berg, C. O.
 1950. *Hydrellia* (Ephydriidae) and Some Other Acalyptrate Diptera Reared from *Potamogeton*. *Annals of the Entomological Society of America*, 43(3):374-398, 4 plates.
- Beyer, A.
 1939. Morphologische, ökologische and physiologische Studien an den Larven der Fliegen: *Ephydra riparia* Fallén, *E. micans* Haliday und *Cänia fumosa* Stenhammar. *Kieler Meeresforschungen*, 3:265-320, 40 figures, 2 tables.
- Brock, M. L., R. G. Wiegert, and T. D. Brock
 1969. Feeding by *Paracoenia* and *Ephydra* (Diptera: Ephydriidae) on the Microorganisms of Hot Springs. *Ecology*, 50:192-200, 4 tables.
- Busacca, J. D., and B. A. Foote
 1978. Biology and Immature Stages of Two Species of *Notiphila*, with Notes on Other Flies Occurring in Cattail Marshes (Diptera: Ephydriidae). *Annals of the Entomological Society of America*, 71(3):457-466, 23 figures.
- Campbell, B. C., and R. F. Denno
 1978. Structure of Aquatic Insect Community Associated with Intertidal Pools on a New Jersey Salt Marsh. *Ecological Entomology*, 3(3):181-188.
- Coquillett, D. W.
 1900. New Genera and Species of Ephydriidae. *The Canadian Entomologist*, 32(2):33-36.
- Cresson, E. T., Jr.
 1915. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae.—II. *Entomological News*, 26(2):68-72.
 1916. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae.—III. *Entomological News*, 27(4):147-152.
 1917. Descriptions of New Genera and Species of the Dipterous Family Ephydriidae.—IV. *Entomological News*, 28(8):340-341.
- Deonier, D. L.
 1971. A Systematic and Ecological Study of Nearctic *Hydrellia* (Diptera: Ephydriidae). *Smithsonian Contributions to Zoology*, 68: 147 pages, 142 figures, 2 tables.
- Deonier, D. L., W. N. Mathis, and J. T. Regensburg
 1979. Natural History and Life-Cycle Stages of *Notiphila carinata* (Diptera: Ephydriidae). *Proceedings of the Biological Society of Washington*, 91(4):798-814, 20 figures.
- Deonier, D. L., and J. T. Regensburg
 1978. Biology and Immature Stages of *Parydra quadrinotata* (Diptera: Ephydriidae). *Annals of the Entomological Society of America*, 71(3):341-353.
- Dowding, V. M.
 1967. The Function and Ecological Significance of the Pharyngeal Ridges Occurring in the Larvae of Some Cyclorrhaphous Diptera. *Parasitology*, 57: 371-388, 7 figures, 2 tables.
- Dumbleton, L. J.
 1969. A New Species of *Ephydrella* Tonnoir and Malloch (Diptera: Ephydriidae) from Hot Springs and Notes on Other Diptera from Mineralised Waters. *New Zealand Entomologist*, 4(2):38-46, 7 figures.
- Eastin, W. C., and B. A. Foote
 1971. Biology and Immature Stages of *Dichaeta caudata* (Diptera: Ephydriidae). *Annals of the Entomological Society of America*, 64(1):271-279.
- Foote, B. A., and W. C. Eastin.
 1974. Biology and Immature Stages of *Discocerina obscurella* (Diptera: Ephydriidae). *Proceedings of the Entomological Society of Washington*, 76(4):401-408.
- Hendel, F.
 1917. Beiträge zur Kenntnis der acalyptraten Musciden. *Deutsche Entomologische Zeitschrift*, 1917(6):33-47, 3 figures.
 1931. Kritische and synonymische Bemerkungen über Dipteren. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 81(1-4):4-19.
- Hennig, W.
 1943. Übersicht über die bisher bekannten Metamorphosestadien der Ephydriden, mit Neubeschreibungen nach dem Material der Deutschen Limnologischen Sundaexpedition (Diptera: Ephydriidae). *Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem*, 10(2/3):105-138, 18 figures, 2 plates.
- Hine, J. S.
 1904. On Diptera of the Family Ephydriidae. *The Ohio Naturalist*, 4(3):63-65.

- Houlihan, D. F.
1969. The Structure and Behavior of *Notiphila riparia* and *Erioptera squalida*, Two Root-piercing Insects. *Journal of Zoology, Proceedings of the Zoological Society of London*, 159:249-267, 19 figures.
- Johannsen, O. A.
1935. Aquatic Diptera, Part II: Orthorrhapha-Brachycera and Cyclorrhapha. *Cornell University Agricultural Experiment Station Memoir*, 177:1-62, 12 plates.
- Johnson, C. W.
1913. The Dipteran Fauna of Bermuda. *Annals of the Entomological Society of America*, 6(4):443-452, 2 figures.
1925. List of the Diptera to Two-Winged Flies. In *Fauna of New England. Occasional Papers of the Boston Society of Natural History*, 7(15):1-326, 1 figure.
- Leonard, M. D.
1928. List of the Insects of New York with a List of the Spiders and Certain Other Allied Groups. *Cornell University Agricultural Experiment Station Memoir*, 101: 1-1121.
- Loew, H.
1864. Diptera Americae septentrionalis indigena: Centuria quinta. *Berliner Entomologische Zeitschrift*, 8: 49-104.
- Mathis, W. N.
1979a. Studies of Notiphilinae (Diptera: Ephydriidae), I: Revision of the Nearctic Species of *Notiphila* Fallén, Excluding the *caudata* Group. *Smithsonian Contributions to Zoology*, 287: 111 pages, 210 figures, 1 table.
1979b. Studies of Ephydrinae (Diptera: Ephydriidae), II: Phylogeny, Classification, and Zoogeography of Nearctic *Lamproscatella* Hendel. *Smithsonian Contributions to Zoology*, 295: 41 pages, 52 figures.
1979c. Ephydrinae (Diptera: Ephydriidae): A New Perspective. In D. L. Deonier, editor, *First Symposium on the Systematics and Ecology of Ephydriidae (Diptera)*. Lawrence, Kansas: The Association of Systematics Collections.
1980. Studies of Ephydrinae (Diptera: Ephydriidae), III: Revisions of Some Neotropical Genera and Species. *Smithsonian Contributions to Zoology*, 303:50, 77 figures.
- Oliveira, S. J. de
1954. Contribuição para o conhecimento do gênero "*Dimecoenia*" Cresson, 1916, I: "*Dimecoenia lenti*" sp. n. encontrada no Chile (Diptera, Ephydriidae). *Revista Brasileira de Biologia*, 14(2):187-194, 19 figures.
1958. Contribuição para o conhecimento do gênero "*Dimecoenia*" Cresson, 1916, IV: Descrição da larva e do pupário de "*Dimecoenia grumanni*" Oliveira, 1954 (Diptera, Ephydriidae). *Revista Brasileira de Biologia*, 18(2):167-169, 5 figures.
- Osten Sacken, C. R.
1878. Catalogue of the Described Diptera of North America. *Smithsonian Miscellaneous Collections*, 16:1-276.
- Ping, C.
1921. The Biology of *Ephydra subopaca* Loew. *Cornell University Experiment Station Memoir*, 49:557-616, 1 figure, 4 plates.
- Simpson, K. W.
1975. Biology and Immature Stages of Three Species of Nearctic *Ochthera* (Diptera: Ephydriidae). *Proceedings of the Entomological Society of Washington*, 77(1): 129-155, 38 figures.
1976. The Mature Larvae and Puparia of *Ephydra (Hal-ephydra) cinerea* Jones and *Ephydra (Hydrotyrus) hians* Say (Diptera: Ephydriidae). *Proceedings of the Entomological Society of Washington*, 78(3):263-269, 14 figures.
1979. Evolution of Life Histories in the Ephydrini. In D. L. Deonier, editor, *First Symposium on the Systematics and Ecology of Ephydriidae (Diptera)*, pages 99-109. Lawrence, Kansas: The Association of Systematics Collections.
- Steyskal, G. C.
1970. The Species of the Genus *Dimecoenia* (Diptera: Ephydriidae) in America North of Panama, with the Descriptions of a New Species. *Annals of the Entomological Society of America*, 63(2):462-465, 6 figures.
- Sturtevant, A. H., and M. R. Wheeler
1954. Synopses of Nearctic Ephydriidae (Diptera). *Transactions of the American Entomological Society*, 79:151-257.
- Trägårdh, I.
1903. Zur Anatomie und Entwicklungsgeschichte der Larve von *Ephydra riparia* Fall. *Arkiv for Zoologi*, 1: 1-42, 4 plates.
- Varley, G. C.
1937. Aquatic Insect Larvae Which Obtain Oxygen from the Roots of Plants. *The Proceedings of the Royal Entomological Society of London*, series A, 12:55-60, 2 figures.
- Wirth, W. W.
1965. Family Ephydriidae. In A. Stone, et al., editors, *A Catalog of Diptera of America North of Mexico United States Department of Agriculture, Agriculture Handbook, Agricultural Research Service*, 276: 1696 pages.
1968. Family Ephydriidae. In N. Papavero, editor, *A Catalogue of the Diptera of the Americas South of the United States*, 77: 43 pages. São Paulo: Departa-

- mento de Zoologia, Secretária da Agricultura.
1971. The Brine Flies of the Genus *Ephydra* in North America (Diptera: Ephydriidae). *Annals of the Entomological Society of America*, 64(2):357-377, 41 figures.
- Wirth, W. W., and A. Stone
1956. Diptera. In R. L. Usinger, editor, *Aquatic Insects of California*, pages 372-482, 64 figures. Berkeley: University of California Press.
- Zavattari, E.
1921. Biologia neritica mediterranea, III: Ricerche morfologiche ed etologiche sul dittero alofilo *Ephydra bivittata* Loew. *R. comitato Talassografico Italiano Memoria*, 83: 58 pages, 5 plates.
- Zetterstedt, J. W.
1837. Conspectus familiarum, generum et specierum dip-
terorum, in fauna insectorum Lapponica descrip-
torum. *Isis* (Oken's), 1837:27-67.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI-36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1 $\frac{1}{4}$ " margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the aligned-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5-9." For alignment and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9 \underline{h} ." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9 \underline{b} ." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.

