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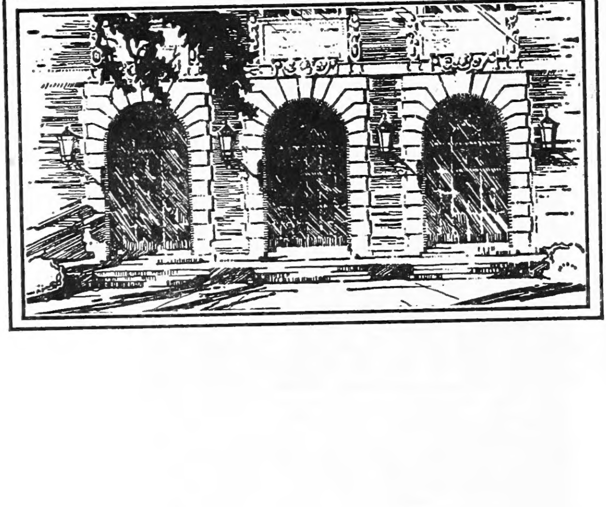

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The Classification, Evolution, and Dispersal of the Winter Stonefly Genus *Allocapnia*

HERBERT H. ROSS and WILLIAM E. RICKER

ILLINOIS BIOLOGICAL MONOGRAPHS 45

UNIVERSITY OF ILLINOIS PRESS

ILLINOIS BIOLOGICAL MONOGRAPHS

Volumes 1 through 24 contained four issues each and were available through subscription. Beginning with number 25 (issued in 1957), each publication is numbered consecutively. No subscriptions are available, but standing orders are accepted for forthcoming numbers. Prices of previous issues still in print are listed below, and these may be purchased from the University of Illinois Press, Urbana, Illinois 61801. Microfilm and photo-offset copies of out-of-print titles in the Illinois Biological Monographs are available from University Microfilms, Inc., 300 North Zeeb Road, Ann Arbor, Michigan 48106, and the Johnson Reprint Corporation, 111 Fifth Avenue, New York, New York 10003.

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UNIVERSITY OF ILLINOIS PRESS URBANA, CHICAGO, AND LONDON

Board of Editors: Donald F. Hoffmeister, Willard W. Payne, Tom L. Phillips, Richard B. Selander, and Philip W. Smith.

This monograph is a contribution from the Illinois Natural History Survey. Issued August 1971.

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CONTENTS

INTRODUCTION

The study reported here had a most unpretentious beginning. During an informal discussion with colleagues in 1956 the question arose: which insect groups have distribution patterns that might contribute reliable information concerning the effect of the Pleistocene glaciers on the biota of eastern North America? Early in the discussion it became clear that highly vagile insects such as winged grasshoppers and leafhoppers disperse so rapidly that their present distribution is largely an expression of ecological rather than historic factors. Certain wingless insects, such as Collembola, have remarkably wide ranges but are easily transported by air currents and are therefore not valid as expressions of historic dispersals within a limited area.

At this point the idea of the cold climates associated with Pleistocene glaciers became associated in our minds with the cold-tolerant stoneflies. A rapid check on some of their distributions as known at that time turned up a most interesting item: the winter stonefly *Allocapnia pygmaea* was primarily a subboreal species in northeastern and eastern North America, but it had an isolated population in the Ozark Mountain area of Missouri. The Missouri population appeared to be a segment of a cold-adapted species left stranded to the south when the remainder of the species moved northward in postglacial times.

Our interest caught by this circumstance, we decided to study the winter stoneflies with special reference to Pleistocene events.

The winter stoneflies belong to a physiologically peculiar group of organisms. With the approach of winter, many living things are normally thought of as becoming quiescent or dormant. In the temperate regions, leaves fall from the trees, the crops are harvested, the sound of crickets declines, and flowers with their attendant multitude of insects disappear from the landscape. For a few insects, however, winter heralds not a cessation but an acceleration of activity. A few crane flies, scorpion flies, caddisflies, and springtails complete their metamorphosis during the cold months of the year and may be found on the snow, on moss beds, or stream banks, where their activity contrasts strikingly with the quiet repose of the great bulk of the insect fauna hibernating in the vicinity.

Among the most abundant of the active winter insects in temperate North America are the winter stoneflies, comprising representatives of several genera belonging to the families Taeniopterygidae, Nemouridae, Leuctridae, and Capniidae, all belonging to the same phylogenetic branch of the insect order Plecoptera (Ricker, 1950; Illies, 1960, 1965).

The genus *Allocapnia* (Figs. 1-3) of the family Capniidae appeared to offer unusually good possibilities for biogeographic interpretation especially with regard to obtaining a better understanding of the evolution of the aquatic fauna of the temperate deciduous forest occurring in the eastern United States and Canada. Before these possibilities could be explored further, it was necessary to re-examine the species composition, phylogeny, and systematic position of *Allocapnia* and its immediate relatives, and attempt to determine the total range of each species. To achieve the last objective, we enlisted the aid of many people in an effort to collect material from the entire eastern part of North America. Over 200 people responded to our request for help. Together they form a group that we call the "Winter Stonefly Club." Most of them, like ourselves, enjoy getting out for a little brisk collecting when the desk chairs in the office begin to harden in January, February, and March. The full list of these collaborators is given in the acknowledgments.

PHYLOGENETIC POSITION OF *ALLOCAPNIA*

The genus being considered here was first described by Claassen (1924) under the name *Capnella,* a name that proved to be preoccupied and for which Claassen later (1928) substituted the new name *Allocapnia.* Until recent years the genus has been considered distinctive, confined to eastern North America, and a close relative of the world-wide genus *Capnia.* There is some question whether it has affinities with the Japanese genus *Takagripopteryx* Okomoto, but we and most authors are of Hanson's (1946) opinion that *Allocapnia* and *Takagripopteryx* are different genera. In an effort to arrive at a better understanding of this problem, we attempted to reconstruct the phylogeny of the Capniidae at least so far as it concerns the North American fauna. In this study we relied heavily on the morphological studies of Hanson (1946). Unfortunately, we were unable to obtain material of the Old World genera that were also unavailable to him, including species placed in *Takagripopteryx.* In this sense the family tree we propose is incomplete, but this should not reflect on its validity as a logical hypothetical beginning.

In comparing various genera of the Capniidae with those of the Taeniopterygidae, Nemouridae, and Leuctridae, it is highly probable that the ancestral Capniidae possessed, among others, the following primitive characters: hind wing with veins R_3 and R_5; metafurcasternum rectangular and the same size as mesofurcasternum; postfurcasternal plates (pfs) separate; vesicle (ventral lobe) present at the anterior margin of the ninth sternite (9S); at least one crossvein present in the costal space; A_1 of fore wing not sharply bent near the Cu-a crossvein; epiproct (supra-anal process) of the male a single structure, undivided.

No living genus of stoneflies is known with this combination of characters. The genus *Isocapnia* has primitive venation and metafurcasternum but has the postfurcasternal plates fused. All the other genera lack veins R_3 and R_5 in the hind wing. From this it seems that the ancestral Capniidae possessed both characters in the ancestral condition and gave rise to two branches, one leading to *Isocapnia* in which only the postfurcasternal plates became changed, and another leading to Ancestor 1 in which the hind wings lost veins R_3 and R_5 (Fig. 4). Ancestor 1 is represented by a persisting branch, the genus *Paracapnia*, that, except for loss of the vesicle, appears to be little changed. In addition it apparently gave rise to Ancestor 2, in which the metafurcasternum became reduced. Ancestor 2 apparently gave rise to three lineages: (1) a line exhibiting little change, represented by the genus *Eucapnopsis;* (2) one in which the postfurcasternal plates became fused and the vesicle and the costal crossvein were lost, represented by the two closely related genera *Capnioneura* and *Nemocapnia;* and (3) a lineage in which the mesofurcasternum became triangular and vein A_1 became bent in the fore wing, evolving into Ancestor 3.

Ancestor 3 gave rise to three lineages, two little changed and represented by the *hingstoni* and *gregsoni* groups of *Capnia,* and a third in which the ventral lobe of the male 9S was lost, resulting in Ancestor 4, represented by some *Capnia* and *Allocapnia.*

The Old World and New World species known to us that apparently arose from Ancestor 4 can be arranged in 10 species groups assigned to the genus *Capnia* plus the genus *Allocapnia,* as indicated in Fig. 4. Of the species groups assigned to *Capnia,* the *bifrons, oenone,* and *melia* groups have no dorsal process on the male seventh and eighth tergites; the remainder have a dorsal process on the male seventh tergite and appear to represent Ancestor 5 in which this structure appeared. In the *excavata, atra, nigra,* and *elongata* groups the epiproct is simple or nearly so, the ancestral condition for the family. In the *manitoba, columbiana,* and *vidua* groups the epiproct is deeply divided, indicating that all three arose from a common progenitor (Ancestor 6) possessing this character. Ancestor 6 gave rise to two lineages. In one, leading to Ancestor 7 (parental to the *manitoba* and *columbiana* groups), the epiproct is V- or U-shaped in profile (Fig. 5).

In the other lineage, leading to Ancestor 8, the epiproct is composed of dorsal and ventral limbs closely appressed and forming a single functional unit. Ancestor 8 gave rise to the *vidua* group and to *Allocapnia*. In both the *vidua* group (Fig. 6) and *Allocapnia,* the dorsal limb of the epiproct has a sharp bend or elbow some distance from the apex; at the apex there is a membranous area surrounding the gonopore, through which the eversible aedeagus is extruded; and the lower limb of the epiproct has a curious apical portion set off by a marked constriction from the long base. The two parts are rigidly joined at the base as a stout curved structure. By force, the two parts may be separated without breaking to an angle of 20 or 30 degrees; when the force is released, the spring tension of the basal loop causes the two parts to snap back together again. It seems highly unlikely that such a complex mating structure would have evolved twice and, on this basis, the only reasonable assumption is that *Allocapnia* arose from a form very much like a primitive member of the *vidua* group. In the *manitoba, columbiana,* and *vidua* groups the male seventh tergite has a dorsal process but not the eighth; in *Allocapnia* the male eighth tergite always has a dorsal process and in all primitive species of the genus the seventh has none. It is evident that in *Allocapnia* the primary dorsal process has moved from the seventh to the eighth segment, as has apparently happened also in some lineages of *Capnia.*

In the groups of *Capnia* having a simple epiproct (*hingstoni* group to *elongata* group in Fig. 4), the base of the ninth tergite has only a thin sclerous thickening along its lateral and dorsal margins (Fig. 7); in the *manitoba* and *columbiana* groups this basal thickening is slightly to moderately strengthened in the mesal region (Figs. 8, 9); in the *vidua* group the lateral portions of the basal thickening are wide, but the mesal part is absent and this portion of the dorsal margin is membranous (Fig. 10); in *Allocapnia* the basal thickening has wide lateral portions and a strong U-shaped sclerous mesal portion (Fig. 11). These structures also support the close affinity of the *vidua* group and *Allocapnia.* It is a simple matter to construct a common ancestral form (Ancestor 8) roughly intermediate between the two and explain the existing structures by postulating an atrophy of the mesal portion in *vidua* and a strengthening and accentuation of this portion in *Allocapnia.*

The chief morphological characteristic setting off *Allocapnia* from *Capnia* is the loss of the sutures of the praescuta on both the meso- and metathorax, together with an associated irregularity of wing venation. Both of these changes are apparently associated with greatly reduced flight potential in *Allocapnia.* The loss of the praescutal sutures is probably associated with the atrophy of muscles involving flight, and the irregularities of venations are probably due to a reduction of selection pressures that would normally maintain the areodynamic pattern of fully functional wings.

Despite its phylogenetic position as a branch of *Capnia,* we believe that *Allocapnia* should be designated as a separate genus because of the many distinctive features that have evolved. This designation of *Allocapnia* as a separate genus without treating other branches of *Capnia* in like manner is an example of paraphyletic classification, strongly criticized by some (Hennig, 1966). There are, however, many well-known examples of it in classification; for example, the recognition of Mammalia, Aves, and Reptilia as separate classes. There is no doubt that paraphyletic classification is a convenience that will continue to have frequent use.

SYSTEMATIC TREATMENT OF *ALLOCAPNIA*

GENUS *ALLOCAPNIA* CLAASSEN

Capnella Claassen (1924:43). Type-species *Capnella granulata* Claassen. Name preoccupied.

Allocapnia Claassen (1928:667). New name.

Diagnosis. In general features, *Allocapnia* is typical of the family Capniidae. It differs from allied genera in that the meso- and metanotum lack praescutal sutures. It differs from all other known members of the family, except *Capnia vidua,* in possessing a double epiproct of distinctive complex structure and from that species it differs in having a dorsal process on the eighth sternite of the male and in the pattern of sclerotization of the male ninth segment (Fig. 11).

Unless otherwise noted in the species accounts, the 38 known species are uniform in shape, size, and color, as follows: length from tip of head to end of abdomen about 5 mm in the male and 6 mm in the female; color dark brown, the wings slightly smoky with brown veins; in the females the wings extend beyond the tip of the abdomen (Fig. 1); in the males the wings vary greatly in length within and among the species (Figs. 2, 3). Known diagnostic characters separating the species occur chiefly in the genital characters associated with the seventh and more posterior segments of the males, and in the seventh and eighth sternites of the females. To date, reliable diagnostic characters for the nymphs are unknown.

Frison (1929, 1935) published considerable biological information concerning members of the genus.

All known species of the genus except *minima* are restricted to the temperate deciduous forest of eastern North America and its ecotone areas with the coniferous forest immediately to the north. The exceptional species *minima* occurs in Quebec almost to the northern limit of trees. The adult emergence of the species is tied closely to the winter season. In the southern states adults emerge from November into January; at the latitude of Illinois, from late November into March; and in southern Canada, principally in March and April with no evidence of an earlier fall emergence. This winter emergence is by no means a unique feature of *Allocapnia;* many other genera of stoneflies share it.

Terminology. Names used in this paper for morphological structures are those employed by Hanson (1946). Parts of the genitalia or associated structures commonly used are indicated in Fig. 12 (male parts) and Fig. 51 (female parts).

Distribution records. For all species the distribution records have been plotted on maps. If we have 10 or less localities from which a species is known, we have cited the complete collection data available. If we have more than 10 records, we have summarized the dates and ecological notes and listed the states and provinces of occurrence. In total we have records from about 3,000 localities (Fig. 87), but many of these are only a few miles apart and impossible to show on a small-scale map. Upon request, a detailed list of records is available from the Illinois Natural History Survey.

Material studied. Material available for study includes the extensive winter stonefly collections assembled by the late T. H. Frison and large recent accessions gathered by the Winter Stonefly Club and our colleagues in the Section of Faunistic Surveys and Insect Identification of the Illinois Natural History Survey. The entire winter stonefly material assembled from eastern North America totals about 250,000 specimens, of which about 150,000 belong to the genus *Allocapnia.* Aside from type-specimens, whose depositories are stated specifically, the majority of this material is in the collection of the Illinois Natural History Survey. The remainder has been returned to the Canadian National Insect Collection, Cornell University, The United States National Museum, and the collections of Dr. S. W. Hitchcock, New Haven, Connecticut, and Dr. P. H. Freytag, Lexington, Kentucky.

Voucher specimens of all but the rarest species have been deposited in the following collections:

Academy of Natural Sciences, Philadelphia, Pennsylvania
American Museum of Natural History, New York, New York
Auburn University, Auburn, Alabama
British Museum (Natural History), London, England
California Academy of Sciences, San Francisco, California
Canadian National Insect Collection, Ottawa, Ontario, Canada
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Field Museum of Natural History, Chicago, Illinois
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Purdue University, West Lafayette, Indiana
University of Georgia, Athens, Georgia
University of Kansas, Lawrence, Kansas
University of Michigan, Ann Arbor, Michigan

Use of the Keys to Species

Characters used in the following keys to the males and females are based on the visibility of diagnostic structures as seen in well-extended specimens or specimens sufficiently pliable that the structures and segments to be seen can be manipulated into a satisfactory orientation. Shrunken specimens cannot be keyed satisfactorily. In the case of the males, satisfactory preparations can be obtained by macerating the abdomen in potassium hydroxide solution, sufficiently to dissolve the viscera to the point that they can be worked out of the specimen, but not enough to cause any drastic loss of color in the integumental structures. Bleaching of very dark specimens to a lighter shade can be accomplished by judicious use of a solution of hydrogen peroxide and ammonium hydroxide. Cleared specimens are best seen as free preparations in glycerine.

Structures of the female are best seen on a well-extended, uncleared specimen. If the specimen is shrunken and difficult to manipulate, the abdomen can be macerated slightly with a potassium hydroxide solution and a fairly satisfactory preparation obtained.

KEY TO SEXES

Dorsum of terminal segments with a complex of structures including a forked sclerous epiproct and a dorsal sclerous projection on at least the eighth tergite (Fig. 12) .... ***males***

Dorsum of abdomen without any processes; eighth sternite modified into a simple subgenital plate of various shapes (Figs. 51-83) .... ***females***

KEY TO MALES

1 Apical segment of upper limb of epiproct longer than basal segment and massive; eighth tergite with a large, flat, cushionlike process and a small anterior process (Fig. 20) .... ***virginiana*** (p. 25)

Apical segment of upper limb of epiproct either much shorter than basal segment (Figs. 38, 43) or not nearly so massive (Figs. 23, 24); eighth tergite either lacking anterior process or with posterior process not forming a large cushion (Figs. 21-49) 2

2(1) Upper limb of epiproct extremely thin, curved up and pointed at tip; process of eighth tergite small and buttonlike (Fig. 19) .... ***loshada*** (p. 25)

Upper limb of epiproct either much thicker, or straight, or depressed at tip (Figs. 15-18); process of eighth tergite either buttonlike or otherwise 3

3(2) Apical segment of upper limb of epiproct long and flat to tip, very thin and regular in profile, and with short dorsal retrorse spines (Fig. 17) 4

Apical segment of upper limb of epiproct either short (Fig. 22), narrow (Fig. 37), or tip expanded (Fig. 15)...6

4(3) Sclerous apex of process of eighth tergite wide, its posterior aspect not appearing to be on an elevation (Fig. 16) .... ***mohri*** (p. 23)

Sclerous apex of process of eighth tergite narrow, from the posterior aspect appearing to be on a high, narrowed elevated portion of the tergite (Fig. 17) 5

5(4) Process of eighth tergite with its apical ridge transverse (Fig. 18) .... ***polemistis*** (p. 24)

Process of eighth tergite with its apical ridge semicircular (Fig. 17) .... ***recta*** (p. 23)

6(3) Dorsal process of eighth tergite forming a wide projection (Figs. 12-15) that is not cleft on meson 7

Dorsal process of eighth tergite cleft on meson, the resultant lobes either close together (Fig. 29) or far apart (Fig. 40) 11

7(6) Dorsal process of eighth tergite with a low, sharp profile (Figs. 12-14) 8

Dorsal process of eighth tergite situated on a definite hump and with a wider or higher profile (Figs. 15, 35) 10

8(7) Wings about half length of abdomen...... ***brooksi*** (p. 19)

Wings vestigial, represented only by minute scales 9

9(8) Apical segment of upper limb of epiproct as long as basal segment (Fig. 14) .... ***tennessa*** (p. 20)

Apical segment of upper limb of epiproct only half as long as basal segment (Fig. 12) .... ***vivipara*** (p. 21)

10(7) Apical segment of upper limb of epiproct extremely short, less than a third length of the basal segment; process of eighth tergite high and angled posteriorly, its opaque tip minute (Fig. 35) .... ***minima*** (p. 38)

Apical segment of upper limb of epiproct at least as long as basal segment; process of eighth tergite with a larger opaque apex (Fig. 15) .... ***malverna*** (p. 22)

11(6) Eighth tergite with a wide, U-shaped, apical incision extending half length of tergite; upper limb of epiproct massive but short (Fig. 43) .... ***perplexa*** (p. 44)

Eighth tergite much less deeply if at all incised; upper limb of epiproct various, often long and not massive 12

12(11) Dorsal process of eighth tergite forming a pair of oblique rugose areas, their dorsal aspect U- or V-shaped (Figs. 21-26) 13

Dorsal process forming a transverse bar or oval having 2 or 3 projecting apical points or lobes (Figs. 27, 30) 18

13(12) A setose process situated just below each lobe of the process of the eighth tergite (Fig. 22) 14

Eighth tergite without such processes (Fig. 21) .... ***fumosa*** (p. 26)

14(13) Profile of dorsal process of eighth tergite fairly long and either declivitous or concave, its anterior corner angulate (Figs. 25-26); dorsal aspect of dorsal process somewhat U-shaped 15

Profile of dorsal process of eighth tergite either much shorter or not declivitous (Figs. 22-24); dorsal aspect of dorsal process with posterior margin angulate or rounded 16

15(14) Lateral aspect of rugose dorsal area of process of eighth tergite almost confluent with outline of dorsal margin of segment (Fig. 25) .... ***frisoni*** (p. 30)

Lateral aspect of rugose dorsal area of process of eighth tergite set off markedly from profile of the anterior portion of the segment (Fig. 26) .... ***peltoides*** (p. 31)

16(14) Apical segment of upper limb of epiproct only as long as basal segment (Fig. 22) .... ***granulata*** (p. 28)

Apical segment of upper limb of epiproct markedly longer than basal segment (Figs. 23, 24) 17

17(16) Apical segment of upper limb of epiproct nearly twice the length of the basal segment and nearly as wide as the lower limb; sclerous portion of dorsal process of eighth tergite more massive (Fig. 24) .... ***unzickeri*** (p. 27)

Apical segment of upper supra-anal process at most 1½ times length of basal segment and much narrower than lower limb; sclerous portion of dorsal process of eighth tergite less massive (Fig. 23) .... ***warreni*** (p. 27)

18(12) Seventh tergite with a sclerotized process either as large as in Figs. 32, 39, or nearly as large as sclerotized portion of process of eighth tergite (Figs. 42, 46, 47) 19

Seventh tergite with no process or with only a small process that is merely a slightly elevated ridge (Figs. 48,49), or process not sclerous (Fig. 28) 30

19(18) Dorsal process of eighth tergite with one mesal and two lateral points (Figs. 39, 46, 47) 20

Dorsal process with only two lateral points (Figs. 44, 45) ... 22

20(19) Posterior aspect of dorsal process of seventh tergite narrow and rounded; tip of lower limb of epiproct with short, deep profile (Fig. 39)...... ***cunninghami*** (p. 42)

Posterior aspect of dorsal process of seventh tergite wide and low, with indications of three dorsal points; tip of lower limb of epiproct with long, slender profile (Figs. 46, 47) 21

21(20) Dorsal process of eighth tergite with mesal point as high as, or higher than, lateral points; lower limb of epiproct with a long, fingerlike tip (Fig. 47) .... ***indianae*** (p. 47)

Dorsal process with mesal point lower than lateral points; lower limb of epiproct tapering evenly to tip (Fig. 46) .... ***ohioensis*** (p. 46)

Some other combination of these two characters........ ....presumed ***indianae*** x ***ohioensis*** hybrids (p. 47)

22(19) Eighth tergite with a small anterior process in addition to a large, wide, incised posterior process..................23
Eighth tergite with only a large posterior process..........24

23(22) Posterior dorsal process of eighth tergite unusually high, its tip angled forward; apical segment of upper limb of epiproct shallow in profile (Fig. 36)....***curiosa*** (p. 39)
Posterior dorsal process low and straight; apical segment of upper limb of epiproct bulbous in profile (Fig. 42) ....***zola*** (p. 43)

24(22) Membranous apex of upper limb of epiproct merging imperceptibly with more sclerous basal portion, its dorsal aspect somewhat bulbous (Figs. 30, 41)................25
Membranous apex of upper limb of epiproct sharply and angularly delineated at base, its dorsal aspect short or diamond-shaped (Figs. 31-34)........................26

25(24) Dorsal process of eighth tergite situated near middle of segment and erect; dorsal process of seventh tergite thin and high (Fig. 41) ....***stannardi*** (p. 42)
Dorsal process of eighth tergite situated near posterior margin of segment, sloping and declivitous; dorsal process of seventh tergite shorter and its sclerous portion smaller (Fig. 30)..............***illinoensis*** (p. 33)

26(24) Process of seventh tergite situated at the middle or on the front half of the tergite, viewed from the side (Figs. 33, 34).......................................27
Process of seventh tergite occupying the rear half of the tergite (Figs. 31, 32)..............................29

27(26) Tip of process of seventh tergite bluntly rounded, not notched; dorsal process of eighth tergite with apex unusually narrow and very shallowly notched (Fig. 34)..28
Tip of process of seventh tergite slightly but distinctly notched; dorsal process of eighth tergite with apex wide and deeply notched (Fig. 33)........***pechumani*** (p. 36)
Intermediates between these two types................ ....***maria*** x ***pechumani*** hybrids (p. 37)

28(27) Dorsal processes of seventh and eighth segments as large as in Fig. 34.........................***maria*** (p. 37)
Dorsal process of seventh segment notably smaller than in Fig. 34; dorsal process of eighth segment narrower, approaching the shape of Fig. 35..................... ....***maria*** x ***minima*** hybrids (p. 37)

29(26) Process of seventh tergite massive and conical; rugose lobes of eighth tergite more prominent (Fig. 31) ....***forbesi*** (p. 35)

Process of seventh tergite small and cleft on meson; rugose lobes of eighth tergite less prominent (Fig. 32) ....***ozarkana*** (p. 34)

30(18) Process of eighth tergite with a mesal point at least half the height of a lateral lobe (Figs. 48, 49) 31

Process either with only two apical lobes (Fig. 44) or with only a minute mesal point between them (Fig. 45) 32

31(30) Profile of dorsal process of eighth tergite as high as wide and without a posterodorsal projecting corner; lower limb of epiproct wider and extending laterally considerably beyond upper limb, the lateral margins often angulate (Fig. 49) ....***nivicola*** (p. 49)

Profile of dorsal process wider, the posterodorsal corner markedly projecting; lower limb of epiproct extending only slightly beyond sides of upper limb (Fig. 48) ....***smithi*** (p. 48)

Profile of dorsal process of eighth tergite narrower, as in Fig. 49, but epiproct as in Fig. 48.................... ....presumed ***nivicola*** x ***aurora*** hybrids (p. 49)

32(30) Apical segment of upper limb of epiproct ovoid in profile and less than one-half length of base (Figs. 38, 40)......33

Apical segment either more slender in profile (Figs. 29, 37) or more than one-half length of base (Fig. 27)......34

33(32) Dorsal process of eighth tergite forming two large, widely separated lobes, divided on meson to basic circumference of segment (Fig. 40)...............***rickeri*** (p. 41)

Dorsal process of eighth tergite not so deeply incised, the two lobes much closer together (Fig. 38)............. ....***sandersoni*** (p. 40)

34(32) Process of eighth tergite with lateral lobes separated by less than half the width of a lobe (Figs. 27-29, 37).......35

Process of eighth tergite with lateral lobes much more widely separated (Figs. 44, 45).......................38

35(34) Apical segment of upper limb of epiproct as long as or longer than basal segment (Figs. 27, 28)...............36

Apical segment of upper limb of epiproct markedly shorter than basal segment (Figs. 29, 37).....................37

36(35) Seventh tergite with a complete sclerotized basal strap and a large apical hump; lower limb of epiproct shorter and relatively deeper (Fig. 28) ....***zekia*** (p. 32)

Seventh tergite with median area membranous, and with little or no hump; lower limb of epiproct longer (Fig. 27) ....***wrayi*** (p. 32)

37(35) Eighth tergite produced into a massive, dorsal, turretlike structure with an extremely steep anterior slope (Fig. 37) ....***jeanae*** (p. 40)

Eighth tergite sloping gradually to dorsal process, not massive (Fig. 29) ....***mystica*** (p. 31)

38(34) Seen from above, process of eighth tergite merging with anterior sclerous band of segment; process only fairly high, its anterior face sinuate, its posterior profile never shouldered (Fig. 45) ....***aurora*** (p. 46)

Process of eighth tergite remote from anterior sclerous band of segment; process high, its anterior face steep, its posterior profile usually shouldered (Fig. 44) ....***pygmaea*** (p. 45)

KEY TO FEMALES

1 Eighth tergite having little or no mesal membranous area, the sclerous portion bridging the entire segment for half or more of its length (Fig. 50A) 2

Eighth tergite having a fairly wide mesal membranous area extending its whole length (Fig. 50B) 5

2(1) Seventh and eighth sternites fused, the mesal portion of the fusion forming a solid longitudinal area in which the intersegmental suture is obliterated (Fig. 52) ....***vivipara*** (p. 21)

A well-marked intersegmental suture or membranous area across the entire mesal area between the seventh and eighth sternites (Figs. 51, 64) 3

3(2) Seventh and eighth sternites solidly fused for about half their width, the line of fusion marked by a short, straight dark line, exactly as in Fig. 51..***tennessa*** (p. 20)

Seventh and eighth sternites joined on meson by only a faintly sclerous strap, the apical margin of the seventh slightly produced and often slightly overlapping the base of the eighth (Figs. 64, 65) 4

4(3) Seventh sternite slightly wider (Fig. 65)..***ozarkana*** (p. 34)

Seventh sternite narrower (Fig. 64) ....***forbesi*** (p. 35)

5(1) Seventh and eighth sternites solidly fused on meson, the line of fusion either not visible (Fig. 71) or indicated by a dark line or crease (Figs. 74-83) 6

Seventh and eighth sternites either completely separated by a membranous area (Fig. 54) or joined on the meson by only a faint semisclerous strap (Figs. 67-68); in some instances of the latter, the seventh sternite has an apical projection extending over the base of the eighth (Figs. 66, 69), and in contracted specimens (Fig. 55) the membrane cannot be seen without manipulation...... 21

6(5) Line of fusion between seventh and eighth sternites not evident on meson, the two sclerites joining without a break in profile (Fig. 73) 7

Line of fusion between seventh and eighth sternites indicated by a dark line and a break in the profile (Figs. 77-83) 10

7(6) Eighth sternite nearly as long as seventh and with its profile sinuate (Fig. 70) .... ***jeanae*** (p. 40)

Eighth sternite much shorter than seventh and with its profile evenly rounded (Fig. 73) 8

8(7) Apex of eighth sternite round (Fig. 74) .... ***stannardi*** (pt.) (p. 42)

Apex of eighth sternite straight (Figs. 71, 73) 9

9(8) Length of well-extended specimen more than 7 mm.................... ***sandersoni*** (p. 40)

Length of well-extended specimen less than 7 mm.................... ***rickeri*** (p. 41)

10(6) Apex of eighth sternite with a wide but shallow sagittate mesal portion contrasting sharply with the much less sclerous remainder of the mesal area of the sclerite (Fig. 63) .... ***illinoensis*** (p. 33)

Mesal area of apex of eighth sternite not contrasting noticeably with the more basal portion of the sclerite..... 11

11(10) Apex of eighth sternite angulate (Figs. 75, 76) 12

Apex of eighth sternite round or truncate (Figs. 74, 77-83) .. 13

12(11) Eighth sternite almost twice as wide as long (Fig. 76) .... ***perplexa*** (p. 44)

Eighth sternite considerably longer (Fig. 75) .. ***zola*** (p. 43)

13(11) Eighth sternite produced into a broad rounded flap capable of being reflexed under the edge of the sternite (Figs. 77, 79) 14

Eighth sternite with apical flap either indistinct (Figs. 80, 81) or narrow and truncate (Figs. 78, 82, 83) 15

14(13) Apical flap of eighth sternite projecting markedly beyond mesal edge of lateral humps, which are chiefly membranous (Fig. 77) .... ***pygmaea*** (p. 45)

Apical flap shorter, the entire sternite sclerous (Fig. 79) .. .. ***ohioensis*** (p. 46)

15(13) Apex of eighth sternite produced into a truncate flap (Figs. 78, 82, 83) capable of folding dorsally under the edge of the sternite; when extended, it reaches considerably beyond the lateral humps of the sternite...... 16

Apex of eighth sternite not so produced.................. 18

16(15) Apical flap of eighth sternite moderately wide, the lateral humps of the sternite chiefly membranous, the combination of the two producing a somewhat hourglass-shaped mesal dark area on the segment (Figs. 78, 82).......... 17

Apical flap of eighth sternite narrower and the lateral humps more extensively sclerotized (Fig. 83)........ .... ***nivicola*** (p. 49)

17(16) Apical flap of eighth sternite longer and narrower, as in Fig. 78.............................. ***aurora*** (p. 46)

Apical flap of eighth sternite shorter and wider, as in Fig. 82 .... ***smithi*** (p. 48)

18(15) Apical flap of eighth sternite arcuate (Fig. 74).......... .... ***stannardi*** (pt.) (p. 42)

Apical flap of eighth sternite indistinct (Figs. 51, 72, 80, 81).. 19

19(18) Lateral areas of eighth sternite light in color, the lateral humps indistinct (Figs. 80, 81) .... ***indianae*** (p. 47)

Lateral areas of eighth sternite dark, the lateral humps often conspicuous (Figs. 51, 72)...................... 20

20(19) Seventh sternite same color and texture as sixth (Fig. 51) .... ***brooksi*** (p. 19)

Seventh sternite darker and more sclerous than sixth, in these respects more like eighth (Fig. 72)............ .... ***cunninghami*** (p. 42)

21(5) Apical margin of seventh sternite produced into a mesal lobe extending over about half of the eighth sternite (Fig. 69).......................... ***curiosa*** (p. 39)

Apical margin of seventh sternite produced no more than as shown in Fig. 66.............................. 22

22(21) Central portion of eighth sternite forming a flat, sclerous area extending full length of sternite and truncate or nearly so at apex (Figs. 66-68) 23

Central portion of eighth sternite with flat area either wedge-shaped (Fig. 57), constricted at middle (Fig. 59), only partially sclerous (Fig. 63), or only indistinctly differentiated from lateral areas except at apex of segment (Fig. 56) 25

23(22) Flat central area of eighth sternite as wide as or wider than lateral humps (Fig. 66) ....***pechumani*** (p. 36)

Flat central area of eighth sternite narrower than lateral humps (Figs. 67, 68) 24

24(23) Flat central area of eighth sternite as narrow as in Fig. 68 ....***minima*** (p. 38)

Flat central area of eighth sternite wider, as in Fig. 67.. ....***maria*** (p. 37)

25(22) Basomesal portion of eighth sternite forming either a narrow or pale strap joining seventh sternite, the fusion line only faintly sclerous (Figs. 56, 63) 26

Seventh and eighth sternites completely separated by membrane (Fig. 54); in contracted specimens (Fig. 55) the membrane cannot be seen without manipulation......27

26(25) Mesal portion of eighth sternite dark and sclerous throughout (Fig. 56) ....***virginiana*** (p. 25)

Mesal portion of eighth sternite with only sagittate apical area dark, remainder much lighter (Fig. 63) ....***illinoensis*** (p. 33)

27(25) Apicomesal portion of eighth sternite differentiated into a sagittate or emarginate, fluted area set off laterally by pale membranous areas (Figs. 57-60) 28

Apicomesal portion of eighth sternite not markedly differentiated from lateral areas (Figs. 53-55) 29

28(27) Apicomesal process of eighth sternite wider, its margin usually truncate or emarginate (Figs. 58, 59) ....

.... ***unzickeri*** (p. 27)

..................................***frisoni*** (p. 30)

Apicomesal process of eighth sternite narrower, usually pointed like a spearhead (Figs. 57, 60) ....

.... ***granulata*** (p. 28)

..................................***peltoides*** (p. 31)

29(27) Apical margin of eighth sternite usually concave, with or

without a projecting, short mesal point or arcuate lobe
(Figs. 53-55) .... ***mohri*** (pt.) (p. 23)
.... ***recta*** (p. 23)
.... ***loshada*** (p. 25)
.... ***polemistis*** (p. 24)

Apical margin of eighth sternite convex (Figs. 61, 62) ....
.... ***wrayi*** (p. 32)
.... ***mystica*** (p. 31)
.... ***malverna*** (p. 22)
.... ***mohri*** (pt.) (p. 23)

Species Accounts

In the following accounts of the species, citations are given only to the more useful taxonomic accounts of each species. Exhaustive lists of references are to be found in the world catalogues of Claassen (1940), Hanson and Aubert (1952), and Illies (1966).

The species of *Allocapnia* sort into 10 groups on the basis of shared peculiar conditions of the male and female terminal segments. Each group is diagnosed briefly and the species treated under each group heading.

Unless specifically mentioned, the eighth female tergite has a wide, membranous mesal stripe as in Fig. 50B.

For ease in comparing the distribution of any one species with that of the genus as a whole, all locality records are shown in Fig. 87.

Type-specimens designated herein are deposited in the collection of the Illinois Natural History Survey.

THE *VIVIPARA* GROUP

This group embraces three species characterized by having no dorsal process on the male seventh tergite, having a low, arcuate dorsal process on the male eighth tergite, the process being relatively sharp in lateral aspect, and in having the female seventh and eighth sternites fused.

Allocapnia brooksi **Ross**

Allocapnia brooksi Ross (1964:169). Original description, ♂.

Diagnosis. MALE (Fig. 13): Wings reaching only to fourth tergite. Dorsal process of eighth tergite with lateral aspect having a short anterior shoulder and sharply pointed tip, its posterior aspect evenly arcuate, the entire structure appearing trianguloid from dorsal view. Epiproct short and stocky, the upper limb with basal and apical segments subequal, the apical segment moderately wide and parallel-sided from dorsal view. FEMALE (Figs. 50B, 51): Seventh and eighth sternites fused for two-thirds of their width, the line of fusion indicated by a thin sclerous line, and the two sclerites separated by a definite but shallow solid valley. Seventh sternite considerably paler than eighth. Eighth sternite heavily sclerotized, the lateral lobes pronounced, the mesal portion of the apical margin little if at all produced.

Distribution (Fig. 88). TENNESSEE: Hawkins Co., creek 2 miles SE Rogersville, January 8, 1965, M. Braasch and D. L. Thomas; Sevier Co. 1, 2 miles W Sevierville, on Rt. 441, Guess Creek. Collected from December 29 to February 1.

To date *brooksi* has been found in only two clear, rapid, large creeks flowing out of the Great Smoky Mountains.

Remarks. This is the only species of the *vivipara* group in which the male has well-developed wings. It would therefore appear to be the most primitive member.

Allocapnia tennessa Ross and Ricker

Allocapnia tennessa Ross and Ricker (1964:90). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 14): Wings vestigial, reduced to minute, inconspicuous lobes. Dorsal process of eighth tergite moderately low, slender and relatively sharp from lateral view, evenly arcuate from posterior view. Epiproct short, the upper limb divided into two subequal segments, the apical one with dorsal aspect fairly wide, its extreme tip often appearing slightly expanded in macerated specimens. FEMALE (Fig. 50A): Eighth tergite entirely sclerous or almost so; seventh tergite frequently chiefly sclerous. Seventh and eighth sternites exactly as in Fig. 51, fused for about half their width, the line of fusion marked by a straight dark line. Eighth sternite heavily sclerotized, the lateral lobes somewhat pronounced, the apical margin very slightly produced.

Distribution (Fig. 88). Known only from the central portion of Tennessee, collected from January 13 to March 28.

This species has been collected principally along moderately small streams, often showing signs of farm pollution.

Remarks. Only slight variation has been detected in the characteristics of the males.

Allocapnia vivipara **(Claassen)**

Capnella vivipara Claassen (1924:46). Original description, ♂, ♀.
Allocapnia vivipara (Claassen): Frison (1929:392; 1935:370). ♂, ♀, nymph.

Diagnosis. MALE (Fig. 12): Wings reduced to minute vestiges (Fig. 3). Dorsal process of eighth tergite moderately low, sharply angled from lateral view, arcuate from posterior view. Epiproct elongate, the lateral aspect of its lower limb with a deep, steplike notch between basal portion and tip; upper limb with apical segment only one-half the length of the basal one, the apical segment somewhat bulbous in side view and tapering in dorsal view. FEMALE (Fig. 52): Wings highly variable in length, varying from long ones that reach the tip of the abdomen to short ones that extend only over the first tergite. Eighth tergite entirely sclerous or nearly so, seventh tergite frequently with much of its area sclerous. Seventh and eighth sternites fused, the line of fusion apparent only at the sides, the central portion of the two segments forming an uninterrupted mesal area. Eighth sternite with humps inconspicuous and apical margin not produced.

Distribution (Fig. 88). Widely distributed in an irregular diagonal band from southern Quebec to eastern Kansas and Oklahoma. Records are available from District of Columbia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Michigan, Minnesota, Missouri, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin; Ontario and Quebec. Seasonal records extend from December 10 to April 28, and have a remarkably similar time span throughout the entire range of the species.

The species is found in streams of various sizes and is particularly abundant in streams heavily loaded with organic material. It is especially tolerant of barnyard pollution.

Remarks. This species exhibits remarkably little variation in structure of male genitalia throughout its geographic range. The female exhibits considerable variation in the amount of sclerotization of the abdominal tergites and in the length of the wings. It might be expected that the more sclerous abdomens would be associated with the shorter wings, but this is not so. In large samples taken in Illinois, Indiana, and New York the relation between different conditions of these characters was found to have an almost random distribution. There was similarly little difference in the proportion of the various character conditions present in populations from other parts of the geographic range. These considerations indicate the northward post-Pleistocene dispersal of the species from an area having populations exhibiting these same arrays of character conditions.

Frison (1935) expressed the belief that the record of "*Capnia minima?* Newport" cited by Walsh (1862) from Rock Island, Illinois, probably referred to *vivipara*.

THE *RECTA* GROUP

The seven members of this group have the dorsal process of the male eighth tergite arcuate or only slightly incised, and situated on a marked posterior elevation of the tergite. The male seventh tergite lacks a process. In the females the seventh and eighth sternites are not fused and the apex of the eighth has few or no modifications.

Allocapnia malverna **Ross**

Allocapnia malverna Ross (1964:170). Original description, ♂.

Diagnosis. MALE (Fig. 15): Wings reaching fifth tergite. Dorsal process of eighth tergite fairly high and abrupt, lateral aspect higher anteriorly, posterior aspect broad and almost truncate. Upper limb of epiproct moderately wide and deep, with the apical portion slightly swollen and the tip somewhat pointed, the apical segment about one and one-half times length of basal segment. FEMALE: Wings extending to or slightly beyond tip of abdomen. Eighth sternite more heavily sclerotized than seventh, the lateral lobes only indistinctly delineated, the apical margin rounded and only very slightly produced, as in Fig. 53; the apical mesal area of the sclerite very dark and polished.

Distribution (Fig. 89). ARKANSAS: Hot Springs Co.: Ten-mile Creek, S of Malvern; Jackson Co., no locality. LOUISIANA: LaSalle Parish: 15 miles SW of Jena; Earl Creek, Whitehall; Vernon Parish: Comrade Creek, Kurthwood; Leesville. TEXAS: Gregg Co., Jct. Rts. US 259 and Tex. 155. Records are from January 2 to February 5. The species frequents small, clear, spring-fed streams.

Originally described from Malvern, Arkansas, this species has since been collected in central Louisiana and eastern Texas. It is probably an early season species, and more collecting in December or January might unearth additional records.

Remarks. At present, females cannot be differentiated from those of *mohri* and *mystica.*

Allocapnia mohri Ross and Ricker

Allocapnia mohri Ross and Ricker (1964:91). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 16): Wings reaching fifth tergite. The dorsal process of eighth tergite fairly high and abrupt, lateral aspect higher anteriorly, posterior aspect broad and arcuate. Upper limb of epiproct with apical segment very long compared to basal one; wide, thin, and parallel-sided, forming an almost spatulate blade having conspicuous short teeth directed basally on its upper surface. Lower limb of epiproct with apical segment short and deep. FEMALE (Fig. 53): Wings extending to or slightly beyond tip of abdomen. Eighth sternite more heavily sclerotized than seventh, the lateral lobes only indistinctly delineated, the apical margin usually rounded and very slightly produced but sometimes slightly concave, the apical mesal area slightly polished.

Distribution (Fig. 89). The species is widely distributed in the Ozark-Ouachita region of Missouri, Arkansas, and Oklahoma, and has been collected from November 13 to March 30. It frequents small, rapid, clear streams with a gravel or rocky bottom.

Remarks. Because of variation in the eighth sternite, females cannot be differentiated reliably from those of *mystica* and *malverna.*

Allocapnia recta (Claassen)

Capnella recta Claassen (1924:44). Original description, ♂, ♀.
Allocapnia recta (Claassen): Frison (1929:395). Nymph, ♂, ♀.

Diagnosis. MALE (Fig. 17): Similar to *mohri* except for dorsal process of eighth tergite, in which the posterior aspect has the mesal portion forming a constricted projection standing up noticeably higher than the lateral portions of the process. FEMALE (Fig. 54): Eighth sternite markedly darker and completely separate from seventh, its apical margin concave to a greater or lesser extent, often with a small point at the center of the concavity.

Two extreme types or forms of males and their intermediates occur in this species. In one (Fig. 17D) the lateral aspect of the dorsal process of the eighth tergite has a fairly sharp angle between the anterior slope of the process and its dorsal margin. This condition is almost exactly as it is in *mohri,* a more primitive relative of *recta,* and is therefore considered and named the ancestral form. In the other extreme (Figs. 17G, H), the dorsal margin of the dorsal process forms a small, declivate hump unlike that in any other known species, and is considered the derived condition of this structure. Intermediate conditions are illustrated in Figs. 17A, E, and F.

Distribution (Fig. 90). The species is abundant throughout most of eastern North America from southern Canada to southern Alabama and from the Atlantic Ocean to eastern Illinois, central Kentucky, eastern Mississippi and western Alabama, including records from the following range: Alabama, Connecticut, District of Columbia, Georgia, Illinois, Indiana, Kentucky, Maine, Maryland, Massachusetts, Mississippi, New Hampshire, New York, North Carolina, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, South Carolina, Tennessee, Vermont, Virginia, West Virginia. The ancestral form is known only from southern Alabama where it forms hybrid swarms with the derived form. North of this area only the derived form has been identified. The total seasonal span is from November 3 to April 17.

The species occurs in fairly rapid, clear, cool streams with a gravel or rocky bottom and is more common than most species of the genus in very small spring-fed brooks.

Remarks. No constant differences have been discovered between females of the two forms or between females of *recta, polemistis,* and variants of *mohri.*

Allocapnia polemistis new species

Male (Fig. 18). Wings reaching seventh tergite. Seventh tergite without dorsal process. Dorsal process of eighth tergite high, its lateral aspect with a sharp anterior projection at tip, its posterior aspect truncate. Upper limb of epiproct wide and flat, the apical segment very long and merging imperceptibly with the basal segment.

Female. Eighth sternite more heavily sclerotized than seventh and completely separate from it, its apical margin arcuately incised as in Fig. 54.

Holotype, male. Alabama: Walker Co., 10 miles NE of Jasper, January 12, 1963, H. H. and J. A. Ross.

Paratypes. Alabama: Marion Co., Winfield, December 3, 1965, H. H. Ross and J. A. Ross, 1 ♂; same data, but December 17, 1967, 1 ♂, 3 ♀; Walker Co., same data as for holotype, 3 ♂, 1 ♀; Walker Co., Sipsey River 5 miles W of Grayson, January 8, 1965, M. M. Hensley and P. W. Smith, 1 ♂; Winston Co., near Natural Bridge, December 17, 1967, H. H. and J. A. Ross, 11 ♂, 7 ♀.

Distribution (Fig. 89). To date, this species has been found only in small, clear, rocky streams, undoubtedly of spring origin, in the Black Warrior Uplift region in northwestern Alabama.

Remarks. This species is a close relative of *recta,* differing from it in the sharp anterior projection of the process of the eighth tergite. No reliable differences have as yet been found to separate females of *polemistis* from those of *recta.*

Allocapnia loshada **Ricker**

Allocapnia loshada Ricker (1952:163). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 19): Wings reaching sixth or seventh segment. Dorsal process of eighth tergite produced high above the rest of the segment, its dorsal tip buttonlike from side view, narrow and very slightly incised medially in posterior view. Upper limb of epiproct with apical segment nearly twice length of basal one, its dorsal aspect narrow, its lateral aspect curved dorsally and ending in a sharp tip. Lower limb of epiproct short, its apex deep. FEMALE (Fig. 55): Eighth sternite more heavily sclerotized and separate from seventh, its posterior margin usually produced into a mesal angulation.

Distribution (Fig. 89). Occurs in the Appalachian area in Tennessee, Virginia and West Virginia, where it lives in small, rapid, rocky streams. Seasonal records extend from January 2 to March 12.

THE *VIRGINIANA* GROUP

This group contains only one species, *virginiana,* characterized by a large, flat, cushionlike dorsal process on the eighth segment (Fig. 20). In the female the seventh and eighth sternites are connected on the meson by a fairly narrow, faintly sclerous area.

Allocapnia virginiana **Frison**

Allocapnia virginiana Frison (1942:269). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 20): Wings reaching to about sixth or seventh tergite. Dorsal process of eighth tergite in profile with a small, low, anterior point, the main body of the process massive and flat, in dorsal view forming a wide, keyhole-shaped cushion, in posterior view wide and definitely cleft on the meson. Epiproct somewhat variable in length, the shorter extreme illustrated in Fig. 20, the slightly longer one by Frison (1942:269, Fig. 35). Upper limb of epiproct with apical segment longer than basal one, deep and wide, the two lateral halves tending to spread apart at the apex in macerated specimens. Lower limb of epiproct with apical segment short and deep. FEMALE (Fig. 56): Eighth sternite more sclerous than seventh, well separated from it by a membranous area except for a short, narrow, faintly sclerous, mesal strap which links the two segments.

Distribution (Fig. 92). Known records occur from the eastern slopes of the Appalachians in northern Virginia to the isolated hill regions of western and southern Alabama, with records from the following states: Alabama, Georgia, Mississippi, North Carolina, South Carolina, and Virginia. Collection dates are from November 22 to February 27.

The species occurs in small, rapid, clear streams with a gravel or rocky bottom.

Remarks. This is the only species in the genus having the dorsal process of the male eighth tergite developed into a large flat cushion. This cushion, however, appears to be a simple derivative of the same type of structure that gave rise to the V- or U-shaped process exhibited by members of the following group.

THE *GRANULATA* GROUP

Members of this group are characterized by lacking a sclerous process on the male seventh tergite, having a curious dorsal process on the male eighth tergite, the process appearing V- or U-shaped from dorsal view (Fig. 21), and in having the female seventh and eighth sternites well separated by membrane. Six species are placed in this group.

Allocapnia fumosa **Ross**

Allocapnia fumosa Ross (1964:174). Original description, ♂.

Diagnosis. MALE (Fig. 21): Wings reaching fourth or fifth segment. Process of eighth tergite high, the entire dorsal part of the segment forming a steep and massive prominence; dorsal rugose areas of the process V-shaped from dorsal view, flanked on each side by a round lobe that is part of the segment and does not form a fingerlike projection. Upper limb of epiproct with apical segment markedly longer than basal one, narrow and parallel-sided in dorsal view; lower limb with apical segment moderately long and of medium depth. FEMALE as yet unknown.

Distribution (Fig. 93). Known only from five localities in or very close to the Great Smoky Mountains of North Carolina and Tennessee, as follows: NORTH CAROLINA: Canton, Haywood Co.; Poison Cove Branch, Henson Cove, Pisgah Creek, Haywood Co. TENNESSEE: 2 miles W of Gatlinburg, Sevier Co.; Great Smoky Mountains National Park, Elkmont, Laurel Branch; Great Smoky Mountains National Park, New Found Gap, Cole Branch. Collection dates are from December 26 to 29.

This species has been found only in fairly large, fast, rocky streams of the creek or small-river size and originating or occurring at high elevations.

Remarks. The lack of setose processes adjacent to the dorsal process of the eighth segment would seem to indicate that *fumosa* is the most primitive member of the *granulata* group.

***Allocapnia warreni* Ross and Yamamoto**

Allocapnia warreni Ross and Yamamoto (1966:265). Original description, ♂.

Diagnosis. MALE (Fig. 23): Wings reaching fifth abdominal segment. Seventh tergite with posterior half forming a rounded but not sclerous bulge. Process of eighth tergite with rugose area markedly raised and sharply set off from contour of anterior part of segment; the pair of small haired projections below the rugose area appears slightly detached from it in dorsal view. Upper limb of epiproct moderately narrow, the apical segment slightly longer than the basal segment; lower limb with apical segment relatively short and deep. FEMALE unknown.

Distribution (Fig. 93). Known only from the holotype male collected along Clear Creek, Washington Co., Arkansas, on January 29.

Remarks. This species is most closely related to *granulata,* differing in the unusually prominent differentiation of the rugose lobes of the eighth tergite, and in the longer, uniformly narrow apical segment of the upper limb of the epiproct.

***Allocapnia unzickeri* Ross and Yamamoto**

Allocapnia unzickeri Ross and Yamamoto (1966:267). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 24): Wings reaching sixth tergite. Seventh tergite with nonsclerous posterior bulge. Process of eighth tergite high and prominent, the large rugose lobes somewhat V-shaped from dorsal view; the pair of haired projections just below them small but prominent. Upper limb of epiproct narrow, the apical segment more than 1½ times the length of the basal segment, its dorsal aspect parallel-sided and slightly spatulate. Lower limb of epiproct with apical segment moderately long and fairly shallow. FEMALE (Fig. 58): Eighth sternite much more sclerous than seventh, from which it is distinctly separated by membrane, its apical margin having a fairly well-defined sclerous mesal portion set off from the surrounding membrane, this mesal portion being of various shapes. The observed extremes are illustrated in Fig. 58.

Distribution (Fig. 93). This species is known from a series of localities in Tennessee confined almost entirely to the eastern edge of the Cumberland Plateau and the Cumberland River valley, collected from December 27 to March 13. Although apparently rigidly restricted in geographic distribution, the species is nevertheless extremely abundant in many of the small, rapid, gravelly or rocky streams in which it has been found.

Remarks. This species is an extremely close relative of *warreni*, sharing with it the long, slender, and parallel-sided upper limb of epiproct. This character groups *warreni* and *unzickeri* together as a pair of sister species separate from *granulata*.

Allocapnia granulata **(Claassen)**

Capnella granulata Claassen (1924:44). Original description, ♂, ♀.
Allocapnia granulata (Claassen): Frison (1929:394; 1935:364), ♂, ♀, nymph.

Diagnosis. MALE (Fig. 22): Wings varying from extremely short, extending only slightly beyond the first abdominal segment to moderately long, reaching the seventh segment. Seventh tergite with nonsclerous posterior bulge. Dorsal process of eighth tergite moderately high, sloping evenly from base, the rugose dorsal area somewhat V-shaped from dorsal view; on each side immediately posterior to this sclerous area there is a short tubercle surmounted by a few fine hairs. Upper limb of epiproct with apical segment slightly to moderately shorter than basal one, spatulate in dorsal view. Lower limb with apical segment moderately long and deep, its tip varying from rounded to bluntly pointed. FEMALE (Fig. 57): Eighth sternite more heavily sclerotized than seventh and separated from it by membrane, its apical portion set off as a moderately wide and angulate sclerous portion well differentiated from the surrounding membrane; the shape of this apical process varies considerably, the commonest type shown in Fig. 57.

Distribution (Fig. 94). Widely distributed over eastern North America, its range forms a broad band extending from southern Quebec and northeastern New York to the Wichita Mountains of Oklahoma, and the pine hills of Louisiana. Records are from the following provinces and states: Ontario, Quebec; Arkansas, District of Columbia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Michigan, Minnesota, Mississippi, New Jersey, Missouri, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin. Collection dates are from December 4 to April 28.

This species frequents larger, slower, and more turbid streams than other species in the genus, in this respect resembling the more widespread members of the Taeniopterygidae. It is the only member of the genus that has been collected as far southwest as the Arbuckle and Wichita Mountains of southern Oklahoma.

Remarks. The species shows considerable variation in three structures of the male genitalia associated with different areas of its range. In eastern populations the profile of the upper limb of the epiproct is more triangular, the tip of the lower limb is broadly rounded, and the sclerous dorsal process of the eighth tergite projects higher above the setate lobes (Fig. 84*a*). In Ozark-Ouachita populations the opposite conditions prevail (Fig. 84*c*). In Wichita Mountain populations an intermediate type occurs, and in populations extending from east-central Missouri through central Illinois one extreme and intermediates may occur together in the same collection.

The male wings vary greatly in length, the longest almost reaching the tip of the abdomen, the shortest being almost scalelike and no longer than the width of the head. In the population from the Wichita Mountains in Oklahoma the wings are uniformly at or near the short extreme. In populations from Virginia southwestward to central Kentucky and Tennessee the wing lengths average near the long extreme. Over the remaining great bulk of the range the wing lengths average near the median for all collections.

By combining histograms for these male characteristics in populations along chosen transects across various parts of the range, Ross and Yamamoto (1967) outlined four modally distinct populations:

Population 1. A southeastern population having long wings and eastern-type genitalia.

Population 2. A central and northern population having median wings and eastern-type genitalia.

Population 3. An Ozark-Ouachita population having median wings and western-type genitalia.

Population 4. A Wichita Mountain population having extremely short wings and intermediate-type genitalia.

Populations 1 and 2 merge into each other almost imperceptibly. Population 4 is highly distinctive because of its short wings, except that a neighboring population in the Arbuckle Mountains of Oklahoma slightly overlaps populations 3 and 4.

Population 3 is also highly distinctive, differing from Population 4 in having longer wings, and from Population 2 in having western-type genitalia. There is some intergradation in every character, however, and no indication of bimodality except in wing length, which appears to be erratic. From this evidence it seems apparent that no genetic discontinuity exists between the four populations.

Allocapnia frisoni Ross and Ricker

Allocapnia frisoni Ross and Ricker (1964:90). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 25): Wings reaching sixth segment. Seventh tergite with only a slight bulge. Dorsal process of eighth tergite with profile flat above and set off sharply from the anterior slope of the segment; a small tubercle below the rugose area at each side. Upper limb of epiproct with apical segment subequal to basal one, clavate from both aspects; lower limb with apex short but also shallow. FEMALE (Fig. 59): Eighth sternite more heavily sclerotized than seventh and separated from it by membrane (Fig. 59A is a slightly contracted specimen in which the membranous separation is hidden); apical margin of eighth sternite forming a well-differentiated, fairly wide sclerous area that is either almost truncate (Fig. 59B) or incised (Fig. 59A).

Distribution (Fig. 93). This species occurs from New York to central Tennessee along the western flanks of the Appalachians, with records from the following states: Kentucky, New York, Ohio, Pennsylvania, Tennessee, and West Virginia. Collection dates are from December 12 to March 20. The species occurs only in rapid, rocky, clear streams.

Remarks. This species and *peltoides* form a distinctive pair of sister species of the *granulata* complex. Males of the two may be separated from other members of the complex by the relatively U-shaped dorsal aspect of the rugose area of the eighth dorsal process.

Allocapnia peltoides Ross and Ricker

Allocapnia peltoides Ross and Ricker (1964:91). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 26): Distinguished from *frisoni,* the preceding species, only in characters of the genital segments, as follows: dorsal process of eighth tergite larger, its lateral aspect with the tips of the rugose area more anterior to the small, haired processes than in *frisoni;* the dorsal aspect forming a larger shield; dorsal aspect of the upper limb of the epiproct almost uniform in width, not tapering at the base as in *frisoni.* FEMALE (Fig. 60): Similar to that of *frisoni* except that the posterior process of the eighth tergite is narrower and more spearhead-shaped.

Distribution (Fig. 93). Known only from the Ouachita Mountains of Arkansas and adjacent Oklahoma with records as follows: ARKANSAS: Mill Creek, Scott Co.; OKLAHOMA: Poteau, Polk Creek, Leflore Co., and 4 miles S of Lewisville, Haskel Co., all on February 10.

This restricted species occurs only in rapid, rocky, clear mountain streams.

Remarks. This species and *frisoni* are a pair of sister species quite distinct from other members of the *granulata* group.

THE *MYSTICA* GROUP

In males of the three species comprising this group, the seventh tergite lacks a dorsal sclerous process, and the eighth tergite is conspicuously produced dorsally and surmounted by a transverse ridge having a mesal cleft. In the female the seventh and eighth sternites are well separated by a membrane.

Allocapnia mystica Frison

Allocapnia mystica Frison (1929:399). Original description, ♂, ♀, nymph.

Diagnosis. MALE (Fig. 29): Wings reaching fifth or sixth segment. Eighth tergite produced into a high sloping dorsal process surmounted by a transverse sclerous ridge that is narrowly cleft on the meson. Upper limb of epiproct with apical segment much shorter than basal one, the whole process spatulate from dorsal view; lower limb with apical segments moderately long and shallow. FEMALE (Fig. 62): Eighth sternite more heavily sclerotized than seventh, its apical margin produced into a rounded, very dark, and highly polished mesal area.

Distribution (Fig. 96). This species is distributed north of the coastal plain from the eastern flanks of the Appalachians through the Ozark-Ouachita area of Missouri and Arkansas, extending north roughly to the line of furthest glacial advance, with a few isolated pockets north of that in Missouri, Illinois, and Indiana. Records are available from the following states: Alabama, Arkansas, Georgia, Illinois, Indiana, Kentucky, Missouri, Ohio, Tennessee, Virginia, and West Virginia. Collection dates are from November 3 to March 29.

The species occurs in cool, rapid, clear, gravelly or rocky streams, usually spring-fed and small. The occurrence of the species in previously glaciated areas is always associated with erosional features in which the gravel and stones of eroded moraines constitute the stream bed.

Remarks. This species is a very close relative of *wrayi* and in a few localities where the ranges of the two abut they occasionally hybridize.

Allocapnia wrayi Ross

Allocapnia wrayi Ross (1964:170). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 27): Similar to *mystica* except for the following characters: Dorsal process of eighth tergite more nearly erect and not sharply angled posteriorly; epiproct shorter, the apical segment of the upper limb as long as the basal one. FEMALE (Fig. 61): Indistinguishable from that of *mystica.*

Distribution (Fig. 96). Common east of the Appalachian Mountains from northern Georgia to about the vicinity of Washington, D.C.; a single record is known from extreme southeastern Tennessee which is west of the Appalachian divide. At this and a similar location in eastern Kentucky *wrayi* hybridizes with *mystica.* Known from District of Columbia, Georgia, North Carolina, South Carolina, Tennessee, Virginia, from December 3 to March 9.

Remarks. This extremely close relative of *mystica* occurs in similar, small, clear, gravelly or rocky streams. In Figs. 61 and 62 the females of *wrayi* and *mystica* appear different, but the much narrower sclerites of Fig. 61 are the result of bilateral compression due to warping.

Allocapnia zekia Ross

Allocapnia zekia Ross (1964:171). Original description, ♂.

Diagnosis. MALE (Fig. 28): Extremely similar to *wrayi,* differing in having a large nonsclerous bulge on the posterior part of the seventh tergite and in having a slightly longer apical segment of the lower limb of the epiproct. FEMALE unknown.

Distribution (Fig. 96). Known only from Maryland on the basis of the holotype male: Zekiah Swamp, La Plata, Charles Co., February 28, 1962, J. Allison, T. Hopkins, R. J. Rubelmann, taken in a cool and presumably spring-fed stream.

Remarks. There is a possibility that this species represents only a local variant of *wrayi*.

THE *ILLINOENSIS* GROUP

The male is characterized by having a dorsal process on the seventh tergite and the upper limb of the epiproct simple and clavate. The female has a faint indication of a sclerous strap between the seventh and eighth sternites. There is only one included species.

***Allocapnia illinoensis* Frison**

Allocapnia illinoensis Frison (1935:365). Original description, ♂, ♀, nymph.

Diagnosis. MALE (Fig. 30): Wings reaching sixth or seventh segments. Seventh tergite produced into a high tubercle that is conical from lateral view, slightly cleft from posterior view, and situated on the posterior half of the segment. Dorsal process of eighth tergite not very high, sloping noticeably posteriorly, its posterior aspect divided by a wide cleft. Upper limb of epiproct with short apical segment which is spatulate from both lateral and dorsal views; lower limb with apical segment shallow. FEMALE (Fig. 63): Eighth sternite slightly more sclerotized than seventh, its lateral lobes distinct, its apical margin produced into a wide sagittate process, dark along the posterior extremity and rapidly becoming less sclerous anteriorly. Seventh sternite with posterior margin slightly arcuate, joined to eighth on the meson by a very faint sclerotized area.

Distribution (Fig. 97). This species is known from only scattered localities widely distributed in southern Canada and northern United States from eastern Minnesota to the Atlantic coast, with isolated records known from southern Wisconsin, central Illinois, and southeastern Ohio. Records are available from the following states and provinces: Illinois, Maine, Minnesota, New York, Ohio, Wisconsin; Ontario, Quebec. Inclusive collection dates are from January 5 to April 2.

In the few localities where the species has been found abundantly it occurs in clear, cool, rocky, spring-fed streams. The probable Pleistocene history of the species has been discussed by Ross et al. (1967:708).

Remarks. In characters of the epiproct this species resembles members of the *mystica* group and it is therefore more primitive than members of the *forbesi* group.

THE *FORBESI* GROUP

In the males of most species comprising this group the seventh tergite has a dorsal sclerous process and the eighth tergite is surmounted by a transverse ridge having a mesal cleft; the upper limb of the epiproct with apical segment very short, often with the apical membranous area delineated sharply at the sides. In the females the eighth sternite is usually joined to the seventh by a faint but distinct semisclerous mesal area.

***Allocapnia ozarkana* Ross**

Allocapnia ozarkana Ross (1964:172). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 32): Wings highly variable ranging from a condition in which they reach the fourth tergite to one in which they are inconspicuous vestiges. Seventh tergite produced into a tubercle not quite as high as that of the eighth, slightly truncate from lateral view and slightly bilobed from posterior view, situated on the posterior half of the segment. Dorsal process of eighth tergite moderately high, sloping posteriorly to a slight degree, its sclerous apex cleft on the meson, appearing as two well-separated rounded lobes from posterior view. Upper limb of epiproct with apical segment very short, the apical membranous portion small, its base narrowed and somewhat wedge-shaped. Lower limb with apical segment moderately narrow and sinuate. FEMALE (Fig. 65): Wings varying from vestigial to a length reaching the sixth segment. Abdomen with three and sometimes four apical dorsal segments sclerous or having only a narrow membranous mesal area. Seventh sternite distinctly more heavily sclerotized than sixth, approaching the texture of the eighth, its apical margin produced into a low, arcuate lobe. Eighth sternite with conspicuous lateral lobes, the central portion somewhat hourglass-shaped, its apex produced into a rounded lobe.

Distribution (Fig. 98). This species is known only from the Ozark uplift in northwestern Arkansas, where it has been collected from January 10 to March 30.

Little is known concerning the habitat of this species. Only a few specimens have been collected, and they may not therefore represent populations from areas in which the species occurs in greatest abundance.

Remarks. This species and the following form a distinctive complex of the *forbesi* group in which both the apterous and winged conditions occur in both the males and the females.

Allocapnia forbesi **Frison**

Allocapnia forbesi Frison (1929:397). Original description, ♂, ♀.
Allocapnia forbesi var. *cornuta* Frison (1935:363). Original description, ♂.

Diagnosis. MALE (Fig. 31): Wings highly variable, ranging between a condition in which they reach the fifth or sixth segment to one in which they are reduced to inconspicuous vestiges. Sixth tergite occasionally with a conical tubercle similar to that of seventh. Seventh tergite produced into a high tubercle conical from both lateral and posterior view, situated on the posterior half of the segment. Dorsal process of eighth tergite high, relatively upright, its posterior aspect divided by a wide cleft and forming two well-separated ovate lobes. Upper limb of epiproct with very short apical segment, the apical mesal membranous area reduced; lower limb with apical segment shallow, almost fingerlike from lateral view. FEMALE (Fig. 64): Wings varying from vestigial to a length reaching the apex of the abdomen. Abdomen with three or four apical dorsal segments sclerous except sometimes having a narrow membranous mesal area. Seventh sternite distinctly more sclerous than sixth, in this respect similar to the eighth, and with its apical margin produced into an arcuate lobe, sometimes as pronounced as in Fig. 64, sometimes less so. Eighth sternite with lateral lobes distinct, the central portion wedge-shaped and produced into a rounded apical lobe. Seventh and eighth sternite usually separated by a membranous area, but in some specimens a very thin hinge line between them appears to be slightly sclerous.

Distribution (Fig. 98). *A. forbesi* is known only from southern Illinois to western West Virginia, the records falling within a narrow oval immediately south of the glacial drift areas except for a single record a few miles north of this line in southwestern Ohio. Records are available from the following states: Illinois, Indiana, Kentucky, Ohio, Tennessee, and West Virginia, from November 30 to April 14. Our records of *forbesi* have come from clear, cool, rocky, spring-fed streams that have a tendency to become dry during the summer months. These streams have a gravel and sand bottom that extends down a considerable distance and the pebbles and sand grains are damp a very short distance below the surface. Presumably during the dry summer period the *forbesi* nymphs migrate downward into this essentially amphibious microhabitat.

Remarks. As noted under the preceding species, *forbesi* and *ozarkana* form a distinctive complex of the *forbesi* group and the two may be ecologically similar. A few specimens of this species from different localities have a conical process on the sixth tergite similar to or smaller than that of the seventh. This is the form described by Frison as *forbesi* var. *cornuta.* As Frison stated, these males are similar in every other respect to typical *forbesi* males with which they have always been collected. It seems therefore that this tubercle of the sixth tergite is a rare mutant form of the species and that the few specimens bearing it do not constitute a separate species.

Allocapnia pechumani **Ross and Ricker**

Allocapnia pechumani Ross and Ricker (1964:88). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 33): Wings reaching fifth or sixth segment. Seventh tergite produced into a high, wide tubercle conical from lateral view, slightly cleft from posterior view, and situated on the anterior half of the segment. Dorsal process of eighth tergite angled slightly forward, from posterior view conspicuously cleft and forming two fairly wide, well-separated lateral lobes. Upper limb of epiproct with apical segment short; its apical membranous area almost enclosed laterally by sclerous boundaries, and having a herringbone texture. Lower limb of epiproct moderately deep, its tip abruptly narrowed into a flat tip. FEMALE (Fig. 66): Seventh sternite more heavily sclerotized than sixth, its apical margin produced into an arcuate lobe extending over the mesal part of the eighth sternite. Eighth sternite with small but well-differentiated lateral lobes, the mesal area wide and flat, its apex truncate or nearly so.

Distribution (Fig. 99). This species ranges from western New York into southern Quebec and New Brunswick, with definite records from only these three states and provinces. The New Brunswick record is based on a population whose genetic composition, with morphological criteria as a measure, is 75 percent *pechumani,* 25 percent *maria.* Two other populations in New Brunswick exhibit an apparent hybrid composition of 75 percent *maria,* 25 percent *pechumani,* and a population from Cape Breton Island, Nova Scotia, appears to be 90 percent *maria,* 10 percent *pechumani.* Eight other collections in southern New Brunswick and the western corridor of Nova Scotia appear to be 100 percent *maria.* Collection dates are from March 4 to April 13.

The two species have a line of slight overlap in the southern portion of their range, but to date we have observed no evidence of hybridization in this area. Abundant collections of both species are available for examination, suggesting that to the south there is a rigid barrier preventing the successful interbreeding of the two entities. This is the reason we are considering that *maria* and *pechumani* are distinct species. It has been taken almost entirely in brooks and small creeks that were clear, rocky or gravelly, and moderately small.

Remarks. This species appears to be the most primitive of a cluster of three embracing *pechumani, maria,* and *minima.*

Allocapnia maria Hanson

Allocapnia maria Hanson (1942:81). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 34): Wings reaching fourth or fifth segment of abdomen. Seventh tergite with a high, somewhat conical tubercle typically narrowed to a minute round tip, uncleft mesally, and situated on the anterior half of the segment. Dorsal process of eighth tergite moderately high, angled slightly anteriorly, from posterior view having an unusually narrow apex slightly cleft on the meson. Epiproct very similar to that of the preceding species. FEMALE (Fig. 67): Wings reaching tip of abdomen. Seventh and eighth sternites similar to those of the preceding species except that the flat mesal area of the eighth sternite is considerably narrowed and is often slightly arcuate posteriorly.

Distribution (Fig. 99). The range of this species extends from northern West Virginia to Cape Breton Island of Nova Scotia, with records from Connecticut, Maine, Maryland, Massachusetts, New Hampshire, New York, Pennsylvania, Vermont, Virginia, West Virginia, New Brunswick, Nova Scotia, and Quebec from February 13 to April 25. North of southern New York all our records are from areas east of the Appalachian Divide. It occurs primarily in clear, cool, rocky or gravelly brooks or small creeks.

Remarks. This species is a close relative of *pechumani* with which it hybridizes in the northern portion of its range (see under *pechumani* above).

A. maria also hybridizes with *minima,* as was first demonstrated by Hanson (1960). The range of *maria* is almost entirely within that of *minima,* and occasional hybrid swarms appear throughout the area of overlap. Hanson found only ten specimens sufficiently intermediate between the two parental types (Fig. 85) to be considered indubitable hybrids, but found evidence of slight introgression when characters were tabulated for large mixed collections of the two species. Our own data match Hanson's figures well. Of several thousand males of *maria* and *minima* examined, only a dozen were indubitable hybrids, but a large number of specimens of *minima* showed a small vestige of a *maria* marker.

Allocapnia minima **(Newport)**

Perla minima Newport (1851:450). Original description, adult.
Capnella incisura Claassen (1924:45). Original description, ♂, ♀.
Allocapnia minima (Newport): Ricker (1938:136). Illustration of type.

Diagnosis. MALE (Fig. 35): Wings reaching fifth or sixth segments. Seventh segment without tubercle. Dorsal process of eighth tergite high, its apex angled slightly posteriorly, narrow from both lateral and posterior aspects. Upper limb of epiproct with apical segment extremely short, at most ⅛ length of total process, tip with almost imperceptible apical membranous area; lower limb with apical segment deep, narrowed at tip into a flat tongue. FEMALE (Fig. 68): Seventh sternite little if at all more sclerous than sixth. Eighth sternite a little but not much more sclerous than seventh, its lateral lobes large and conspicuous; between them is situated a flat mesal portion which is very narrow but almost parallel-sided and with its tip truncate or nearly so.

Distribution. (Fig. 100). This is the most northern of the known species of *Allocapnia*, extending from eastern Minnesota to the Atlantic, its southern boundary coinciding roughly with that of the hardwood-coniferous ecotone area, with records in Quebec as far north as 57° latitude, which is close to the tundra area. This is the only species of the genus known from Newfoundland, where it is abundant and widely distributed. Records are from Connecticut, Maine, Massachusetts, Michigan, Minnesota, New Hampshire, New York, Vermont, Wisconsin; Newfoundland, New Brunswick, Nova Scotia, Ontario, and Quebec. Collection dates are from January 5 to May 12.

The species occurs only in large, clear, rocky and very rapid rivers or large creeks. Except in Newfoundland and the recorded localities north of 50° latitude, it has almost invariably been found in association with *pygmaea*.

Remarks. This is a close relative of *maria* whose possible ancestry and origin is discussed later in the consideration of phylogeny.

Allocapnia curiosa **Frison**

Allocapnia curiosa Frison (1942:268). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 36): Wings reaching fifth or sixth segment. Seventh tergite produced into a high tubercle whose apex is oblique from lateral view, rounded from posterior view, and situated on the anterior half of the segment. Eighth tergite with two processes, the anterior, somewhat thumblike one angled anteriorly; the primary dorsal process is also angled slightly anteriorly and from posterior view is divided by a wide cleft into two lateral lobes. Upper limb of epiproct with apical segment only about $\frac{1}{5}$ length of the process, forming a somewhat diamond-shaped structure with a herringbone pattern in the apical dorsal membrane. Lower limb of epiproct highly sinuate, its apical segment large and deep, with the tip narrowed into a thin apical tongue. FEMALE (Fig. 69): Wings reaching end of abdomen. Seventh sternite as heavily sclerotized as eighth, much more than sixth, its posterior margin projected as a rounded lobe well over the base of the eighth. Eighth sternite with well-marked lateral lobes, mesal portion flat, narrowed anteriorly and rounded posteriorly.

Distribution (Fig. 98). The species occurs from the eastern Cumberland Plateau area of eastern Tennessee to southern New York, associated with semimountainous terrain throughout its range. Records are available from Kentucky, Maryland, New York, Pennsylvania, and West Virginia, from January 25 to April 19.

The species is confined to rapid, cool, rocky, semimountainous streams of medium size.

Remarks. This species is a peculiar offshoot of the *pechumani* complex. It has evolved unusual and striking modifications in the genital structures of both sexes.

THE *JEANAE* GROUP

In the male of the sole known species of this group the dorsal process of the eighth tergite is unusually high and the sclerous tip is narrowly incised on the meson. The epiproct is unusually long and slender; the apical segment of its upper limb is only slightly widened toward the tip. In the female the seventh and eighth tergites are fused.

Allocapnia jeanae Ross

Allocapnia jeanae Ross (1964:171). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 37): Wings just barely reaching fourth segment. Seventh tergite without dorsal process. Process of eighth tergite high, steep, and massive; its lateral aspect almost as wide as the tergite is long, the rugose lobes placed far forward, separated by a deep but narrow cleft; the posterior corners of the process forming almost right-angled lobes. Basal segment of the upper limb of the epiproct greatly elongated, about three times as long as the apical segment; apical segment relatively short, slender and slightly clavate from both lateral and dorsal aspects. Lower limb of the epiproct narrow from dorsal view, unusually deep from lateral view. FEMALE (Fig. 70): Wings reaching apex of abdomen. Seventh and eighth segments solidly fused, the line of fusion indicated only by a slightly darker sclerotization of the area but not by a furrow, the lateral view of the venter constituting a continuous sinuate outline; area of fusion occupying not quite half of the total width of the segments. Eighth sternite with lateral lobes indistinct, the apical margin forming a wide produced area that is truncate at apex and irregularly and transversely rugose.

Distribution (Fig. 101). Known only from the northwestern portion of the Ozark uplift area of Arkansas. Although its total known range is small, it has been collected from a considerable number of localities, in each case associated with a rapid, cool, gravelly or rocky creek, probably spring fed, from January 10 to February 14.

Remarks. This species is apparently a very early offshoot of the line leading to the *rickeri* group.

THE *RICKERI* GROUP

In members of this group the apical segment of the upper limb of the epiproct is rather short, freely articulated with the basal segment and almost bulbous from lateral view. In the females the seventh and eighth sternites are solidly fused, the line of fusion often delineated by a heavily sclerotized furrow.

Allocapnia sandersoni Ricker

Allocapnia sandersoni Ricker (1952:165). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 38): Wings extending to fourth or fifth segment. Process of eighth tergite situated on a high, somewhat triangular elevation of the segment, its tip pointed from lateral view, deeply incised and appearing as two widely separated subtruncate lobes from posterior view. Upper limb of epiproct with apical lobe very short, somewhat diamond-shaped from dorsal view, ovate from lateral view; lower limb with its basal portion long and narrow, enlarging conspicuously at its apex where it joins the shallow and sinuate apical segment. FEMALE (Fig. 71): Seventh and eighth sternites solidly fused with no sign of a dividing suture across the mesal half of the area of juncture. Eighth sternite with its apex almost truncate.

Distribution (Fig. 103). Known only from the Ozark uplift, with a single record from southern Missouri and many records from extreme northwestern Arkansas, collected from January 10 to February 18.

Remarks. This species appears to be one of the most primitive of the complex that contains this and the following five species. The female is remarkably similar to that of *rickeri*, differing chiefly in the size measurements given in the key. It occurs in rapid, rocky, cool, spring-fed small creeks.

***Allocapnia rickeri* Frison**

Allocapnia pygmaea Frison (1929:396; 1935:367). Misidentification.
Allocapnia rickeri Frison (1942:269). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 40): Wings reaching fourth or fifth segment. Process of eighth tergite rather low, from posterior view divided by a very wide and deep valley into two lateral, widely separated fingerlike lobes. Upper limb of epiproct with apical segment about one-fourth the length of the entire process, diamond-shaped from dorsal view, almost ovate from lateral view; lower limb with apical segment fairly shallow and slightly sinuate. FEMALE (Fig. 73): Seventh and eighth sternites solidly fused for about three-quarters of their width with no evidence of the suture in the area of fusion. Eighth sternite with lateral lobes usually slightly lighter than mesal portion, apical margin truncate or slightly arcuate.

Distribution (Fig. 102). Widely distributed north of the Gulf Coastal Plain area and south of the glacial plain area from eastern Kansas and Oklahoma through to the Atlantic coast, with isolated records at various localities to the north. Records are available from Alabama, Arkansas, District of Columbia, Georgia, Iowa, Indiana, Kansas, Kentucky, Maryland, Minnesota, Mississippi, Missouri, New Jersey, New York, North Carolina, Ohio, Oklahoma, Ontario, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin. The species has been collected from December 15 to April 19 in clear, cool, rocky or gravelly streams.

Remarks. This widespread species is remarkably uniform morphologically throughout its entire range.

Allocapnia stannardi **Ross**

Allocapnia stannardi Ross (1964:174). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 41): Wings reaching fifth tergite. Seventh tergite with a high process, its lateral view narrow and sharp, its posterior view wide, parallel-sided, and cleft at apex. Process of eighth tergite moderately high and divided into a pair of widely separated, somewhat conical lateral lobes. Upper limb of epiproct with apical segment about one-third length of entire process, wide and diamond-shaped from dorsal view, swollen from lateral view. FEMALE (Fig. 74): Seventh and eighth sternites solidly fused for about three-quarters of their width, the line of fusion indicated in some specimens by a slight indentation and a faint dark line, in other specimens completely indistinguishable either by color or irregularity of the contour of the combined segments. Eighth sternite with lateral lobes moderately well differentiated, the mesal margin slightly arcuate.

Distribution (Fig. 103). Known only from the Great Smoky Mountain region of Tennessee and North Carolina, where it has been taken only in the rapid rocky cascades in the higher elevations. It may be the only species of the genus rigidly confined to this habitat. Collection dates are from December 26 to April 3.

Remarks. This species appears to be a close relative of *rickeri,* differentiated by the very large process of the seventh tergite in the male and by the arcuate apex of the eighth sternite in the female.

Allocapnia cunninghami **new species**

MALE (Fig. 39). Wings reaching fifth abdominal segment. Sixth tergite with a raised anterior swelling not more sclerous than the adjacent tergite. Seventh tergite with a small sclerous tubercle, slightly pointed from lateral view, rounded from posterior view, situated on the anterior half of the segment. Process of eighth tergite only moderately high, the lateral aspect rounded, the posterior aspect trilobed, the two lateral lobes much higher than the small pointed mesal lobe. Epiproct rather long, both arms with a narrow dorsal aspect. Upper limb with apical segment less than one-third length of entire structure, the apical segment ovate from lateral view. Lower limb with apical segment broad basally, tapering to the narrow tip.

FEMALE (Fig. 72). Wings reaching apex of abdomen. Seventh and eighth sternites solidly fused, the line of fusion marked by an arcuate, heavily sclerotized furrow. Eighth sternite with lateral lobes conspicuous and large, mesal area narrow, apical margin of segment truncate.

Holotype ♂.—TENNESSEE: Sumner Co., Turners, small, rapid, gravelly branch, March 14, 1964, H. B. Cunningham. *Paratypes.*—KENTUCKY: Cumberland Co., Bow, Cash Creek, December 30, 1964, H. H. Ross and R. T. Allen, 1 ♂. TENNESSEE: Sumner Co., same data as for holotype, 50 ♂, 12 ♀; 3 miles S of Westmoreland, at clear stream, March 14, 1964, H. B. Cunningham, 1 ♀; same data but 3 miles N of Westmoreland, March 1, 1966, G. L. Rotramel and J. D. Unzicker, 1 ♀.

Distribution (Fig. 103). To date, this species appears to be a local relict confined to the karst country along the Kentucky-Tennessee line. It has been taken only in spring-fed streams.

Remarks. The phylogenetic position of *A. cunninghami* is enigmatic. The general conformation of the male genitalia, especially the short clavate apical segment of the upper limb of the epiproct, indicates a relationship with the *rickeri* group, but the median tooth of the dorsal process of the male ninth tergite suggests affinity with more derived members of the *pygmaea* group.

Allocapnia zola **Ricker**

Allocapnia zola Ricker (1952:166). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 42): Wings reaching fourth or fifth segment. Seventh segment with a low, wide, bilobed dorsal tubercle near middle and a low bilobed elevation on the anterior antecostal ridge. Dorsal process of eighth tergite low, wide, and bilobed; anterior to it is a wide bilobed elevation on the antecostal ridge. Upper limb of epiproct with a long base and short, knobbed apical segment; lower limb with apical segment short and moderately deep. FEMALE (Fig. 75): Seventh and eighth sternites both heavily sclerous and fused for three-fourths of their width, the line of fusion marked by an arcuate sharp crease. Eighth sternite shorter and wider than seventh, its apical margin slightly angulate, the lateral lobes inconspicuous.

Distribution (Fig. 103). This species occurs in a diagonal band from the southwestern flanks of the Appalachians to the hill country of

Maine and New Brunswick. Records are from Connecticut, Kentucky, Maine, New York, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, and New Brunswick, from December 26 to April 13. The species occurs in medium to large creeks and small rivers that are clear, rapid, and rocky.

Remarks. This species rivals *curiosa* in the development of dorsal processes, but is readily differentiated from that species by its bulbous upper limb of the epiproct.

Allocapnia perplexa **new species**

MALE (Fig. 43). Wings short, reaching only to third segment. Seventh tergite having no dorsal process. Dorsal process of eighth tergite relatively low, its lateral aspect oblique. Posterior margin of the tergite deeply and broadly incised, the incision dividing the dorsal process into two lateral lobes. Epiproct with upper limb massive, its apical segment short, its profile somewhat bulbous; lower limb small, narrower than upper and not visible from above.

FEMALE (Fig. 76). Wings almost reaching apex of abdomen. Seventh and eighth segments unusually wide, fused for two-thirds of their width, the line of fusion marked by a sharp crease. Apex of eighth sternite broadly angulate.

Holotype ♂, and 3 ♂, 1 ♀, *paratypes.*—TENNESSEE: Trousdale Co., 5 miles S of Bransford, at murky stream, March 14, 1964, H. B. Cunningham.

Distribution. Known only from this collection (Fig. 103).

Remarks. The peculiar, incised eighth tergite and massive epiproct differentiate this species immediately from all other described forms. The placement of the species is difficult. The female shows considerable similarity to that of *cunninghami,* and the short, large apical segment of the upper limb of the epiproct is suggestive of the *rickeri* group. The species is placed here in the *rickeri* group on these somewhat tenuous grounds.

THE *PYGMAEA* GROUP

In this group the dorsal process of the male eighth tergite is transverse and notched, and may have a mesal tooth arising from the base of the notch. The apical segment of the upper limb of the epiproct is equal in length or nearly so to the basal segment. In the female, the seventh and eighth sternites are fused, the line of fusion marked by a crease, and all but the last two tergites have a wide, mesal membranous area. Six species are included.

***Allocapnia pygmaea* (Burmeister)**

Semblis pygmaea Burmeister (1839:874). Original description, ♂.
Allocapnia torontoensis Ricker (1935:257). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 44): Wings reaching sixth or seventh segment. Seventh tergite without a dorsal process. Dorsal process of eighth tergite fairly high and in profile almost invariably with a setose subangulate shoulder of the segment posterior to it. Process deeply incised, the incised portion no wider than the width of a lateral lobe. Epiproct relatively long; apical segment of upper arm longer than basal one, its dorsal aspect tapering; lower limb just beyond middle wider than upper, tapering to a triangular apex. FEMALE (Fig. 77): Wings extending to apex of abdomen. Apex of eighth sternite wide; the end one-fifth is capable of bending and reflexing beneath the end of the segment.

Distribution (Fig. 104). This is a subboreal species of southern Canada and northern United States with scattered records south through the Appalachians and the Cumberland Plateau to southern Tennessee, and with isolated populations in the Ozark Mountains of Missouri. Records are from Connecticut, District of Columbia, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New York, Pennsylvania, Rhode Island, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin; New Brunswick, Nova Scotia, Ontario, and Quebec. Inclusive collection dates are December 30 to April 26.

A. pygmaea is found in abundance only in large, fast, rocky streams that are cold or cool the entire year. The more southern records to the east are associated with large, spring-fed, "blue-water" creeks of considerable size. The populations located in Missouri occur only in the small but fast and cold rivers having their origin in the extremely large springs typical of that area.

Remarks. The unusual relict populations in Missouri led Ross et al. (1967) to study the intraspecific variation within the whole geographical range of *pygmaea.* This variation proved to be small, expressed chiefly in proportions of different parts of the epiproct. Although the interpopulation variation was smaller than that found in *granulata* (cf. Fig. 84), the Missouri populations differed modally from all other populations considered collectively. From this circumstance it was adduced that the more northern populations of the species had arisen from more eastern preglacial elements of the species (Ross et al., 1967).

In the past, several species have been misidentified as *pygmaea.* Up to 1925 and later, a number of species were lumped together under this name, including all herein-recognized species of the *pygmaea* group and several species of the *rickeri* group. Contributing to the confusion were the small and extremely dark parts offering diagnostic characters, the difficult techniques required to obtain satisfactory study preparations, and the lack of appreciation of glycerine as a temporary study medium. Early discriminatory efforts (Ricker, 1935) first differentiated between what is now considered *pygmaea* and *rickeri*; this was somewhat obscured by the fact that Frison (1942) provided illustrations of *pygmaea*, but his illustrations of male parts refer to *nivicola*, and only his illustration of female parts refers to *pygmaea*. Hanson (1942) first irrevocably gave characters to differentiate *nivicola*, and since then the species in the group have been successively identified.

Allocapnia aurora Ricker

Allocapnia aurora Ricker (1952:159). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 45): Indentical to *pygmaea* except as follows: Seventh tergite sometimes with a very small dorsal process (insets, Fig. 45). Dorsal process of eighth tergite with mesal incision markedly wider than width of a lateral lobe, and sometimes having a minute medial tooth (Fig. 45C). Lower limb of epiproct narrow, only slightly wider than upper limb. FEMALE (Fig. 78): Apex of eighth sternite with reflexing flap much narrow than in *pygmaea*.

Distribution (Fig. 105). This species occurs primarily in the southern Appalachian region from Maryland to southern Alabama. Records are for Alabama, District of Columbia, Georgia, Maryland, North Carolina, South Carolina, Tennessee, Virginia. Inclusive collection dates are December 9 to April 19.

Like *pygmaea*, this species occurs in moderately large, fast, rocky, cool streams. The differences in range are indicative that *aurora* is adapted to streams that may reach higher summer temperatures than those frequented by *pygmaea*. Neither species occurs in the cascadelike courses of the higher Great Smoky Mountain streams inhabited by *stannardi*.

Remarks. The heterozygous condition for a minute dorsal process on the seventh tergite and for the minute mesal projection on the dorsal process of the eighth tergite may be an indication of hybridization between this species and *nivicola*.

Allocapnia ohioensis Ross and Ricker

Allocapnia ohioensis Ross and Ricker (1964:92). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 46): Identical to *aurora*, except as follows: Seventh tergite with a distinct dorsal process that is a caricature of that on the eighth, being trilobed and situated toward the posterior portion of the segment. Dorsal process of eighth tergite always with a moderately large mesal process that is lower than the lateral lobes. Upper limb of epiproct with apical segment markedly shorter than basal one; lower limb with widest point much wider than upper limb. FEMALE (Fig. 79): Reflexing flap of eighth sternite as wide as in *pygmaea* but considerably shorter.

Distribution (Fig. 106). This species has a relatively small range extending from central Kentucky to central New York. Records are from Indiana, Kentucky, New York, and Ohio, from January 5 to March 27. It is associated with small, gravel-bottomed creeks having a moderate volume of flow and probably maintained at a relatively even temperature during summer by spring-fed tributaries.

Remarks. The relatively short but wide reflexed apical part of the female eighth sternite indicates an affinity between this species and *pygmaea* on the one hand and *smithi* on the other.

Allocapnia indianae **Ricker**

Allocapnia indianae Ricker (1952:162). Original description, ♂, ♀.

Diagnosis. MALE (Fig. 47): Similar to *ohioensis* except as follows: Dorsal process of eighth tergite with the mesal projection higher than the lateral lobes; apical segment of lower limb of epiproct with its apex forming a long, narrow fingerlike tip. FEMALE (Figs. 80, 81): Apex of eighth sternite without a reflexible tip, its apical margin either straight (Fig. 80) or with the mesal portion membranous (Fig. 81).

Distribution (Fig. 107). Almost identical with that of *ohioensis*, with records from Indiana, Kentucky, New York, and Ohio, taken from December 30 to April 2. The species *indianae* inhabits essentially the same type of clear, swift, gravel-bottom stream as does *ohioensis*.

Remarks. Although this species and *ohioensis* are obviously closely related sister species inhabiting the same streams, there is excellent morphological evidence that the two represent independently evolving lineages (Ross & Freytag, 1967). In the extensive series of the two obtained to date, including 326 specimens of *indianae* and 149 of *ohioensis* and many collections having both species collected simultaneously, only a single putative hybrid specimen was obtained, a hybrid ratio of 1:474. Local stress mating alone could account satisfactorily for this ratio.

Allocapnia smithi new species

MALE (Fig. 48). Wings long, reaching seventh segment. Seventh tergite with a low transverse process. Dorsal process of eighth tergite low, its profile longer than high, with the posterior corner somewhat angular; posterior aspect with three points, the mesal one slightly higher than the lateral ones. Upper limb of epiproct with apical segment subequal to basal one; lower limb narrow, usually no wider than upper limb, the apex tapering gradually to tip.

FEMALE (Fig. 82). Wings reaching to or beyond apex of abdomen. Seventh and eighth sternites fused for most of their width, the line of fusion indicated by a sharp crease. Eighth sternite with lateral areas submembranous; apical margin produced into a wide, sclerous reflexible flap.

Holotype ♂.—KENTUCKY: Butler Co., 2½ miles W of South Hill, March 29, 1964, P. W. Smith and M. Braasch. *Paratypes.*—ALABAMA: Cullman Co., 4 miles W of Cullman, December 17, 1967, H. H. and J. A. Ross, 1 ♂; Walker Co., 2 miles S of Dora on Ala. 81, January 14, 1966, H. B. Cunningham, 1 ♂, 1 ♀. Winston Co., 5 miles W of Grayson, Sipsey River, January 8, 1965, M. M. Hensley and P. W. Smith, 1 ♂, 1 ♀. ILLINOIS: Pope Co., 5 miles SE Eddyville, Lusk Creek, March 5, 1958, H. H. Ross and L. J. Stannard, 3 ♂; same but February 20, 1969, L. J. Stannard, 1 ♂. KENTUCKY: Butler Co., Dereedy Creek, 6 miles SE of Love, March 29, 1964, P. W. Smith and M. Braasch, 10 ♂, ♀; same but 3 miles SE of Love, 8 ♂ ♀; Creek, 6 miles W of Round Hill, March 29, 1964, P. W. Smith and M. Braasch, 10 ♂; 1 mile E of Round Hill on Rt. 70, January 27, 1966, G. L. Rotramel and I. M. Seligman, 1 ♂; 2½ miles W of South Hill, March 29, 1964, P. W. Smith and M. Braasch, 3 ♂, 2 ♀. Cumberland Co., Creek, 5½ miles SE of Burksville, January 27, 1965, M. E. Braasch and D. L. Thomas, 2 ♂. Edmonson Co., Cub Creek, 3 miles E of Round Hill, March 29, 1964, P. W. Smith and M. Braasch, 2 ♂; E of Round Hill, January 25, 1965, M. E. Braasch and D. L. Thomas, 1 ♂; Creek 8 miles S of Shrewsbury, January 29, 1965, M. E. Braasch and D. L. Thomas, 1 ♀. Grayson Co., Caney Creek, ½ mile S of Spring Lick, January 26, 1965, M. E. Braasch and D. L. Thomas, 1 ♂. Marshall Co., 3 miles W of Benton, Gibson Creek bridge, January 22, 1964, M. Braasch, P. W. Smith, and L. J. Stannard, 10 ♂. Ohio Co., Adams Creek, 4 miles NE of Fordsville, January 26, 1965, M. E. Braasch and D. L. Thomas, 2 ♂. OHIO: Warren Co., deep ravine SE side of Ft. Ancient, February 12, 1966, F. J. Moore, 1 ♀.

Distribution. This species has a small total range (Fig. 108) and is associated with small spring-fed creeks.

Remarks. The male of *smithi* is most similar to that of *nivicola,* from which it differs chiefly in the peculiar profile of the dorsal process of the eighth tergite. The female is similar to that of *aurora,* differing in having the apical flap of the eighth sternite slightly wider and shorter.

Allocapnia nivicola **(Fitch)**

Perla nivicola Fitch (1847:278). Original description, ♂, ♀.
Allocapnia nivicola (Fitch): Hanson (1942:83). Redescription.

Diagnosis. MALE (Fig. 49): Similar to *A. smithi,* the preceding species, except as follows: dorsal process of eighth tergite with profile higher than long, without a posterior angulation, its posterior aspect with mesal tooth usually slightly lower than lateral ones. Lower limb of epiproct much wider than upper limb. FEMALE (Fig. 83): Apex of eighth sternite with flap no wider than illustrated, sometimes narrower.

Distribution (Fig. 109). This is an abundant species from the Maritime Provinces of Canada, southwestward to northern Alabama, with outlier populations in several states. Records are from Alabama, Connecticut, District of Columbia, Illinois, Indiana, Kentucky, Maryland, Massachusetts, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin; New Brunswick, Nova Scotia, and Quebec. Collection dates are from December 5 to April 19.

In contrast to the large-stream propensity of *pygmaea, nivicola* occurs almost entirely in small stony brooks. In both the southern and northern extremes of its range these are spring fed, a condition ameliorating extremes of winter cold to the north and summer heat to the south.

Remarks. Many earlier collections of *A. nivicola* were recorded as various species of the *rickeri* or *pygmaea* groups. The illustrations of the male genitalia ascribed to *pygmaea* by Frison (1942:266, Fig. 33) are *nivicola,* but the female illustrations are *pygmaea.*

A series of collections (marked with an "x" in Fig. 105) differ from those taken in other parts of the range in having the lower limb of the epiproct narrow, as in *smithi* or *aurora.* Both wide and narrow conditions may be found in each collection. There is a possibility that these collections represent hybrids between *nivicola* and some other species, of which *smithi* and *aurora* would be the chief suspects. Evidence of slight introgression in *aurora* but none in *smithi* suggests the former as the probable other parent.

PHYLOGENY

When one considers the present distribution of the species of *Allocapnia* and the fact that many of these species occur in areas that were covered with glacial lobes of the last Ice Age until only 8 or 10 thousand years ago, it is clear that present distribution patterns resulted from different past patterns. To obtain some basic insight into these changing patterns of distribution, it is necessary to view them in relation to the phylogeny of the species involved. In the winter stoneflies, such a phylogenetic inquiry must be based on the evidence of comparative anatomy because other avenues of investigation are as yet not available.

ANCESTRAL CHARACTER CONDITIONS

The crux of adducing phylogeny from comparative anatomy lies in obtaining firm evidence as to what was the ancestral and what is the derived condition of various structures or characteristics. This evaluation can best be achieved by two comparisons; first, looking for conditions that are common to some members of the various species groups of *Allocapnia,* and, second, comparing results of this survey with similar comparisons in species of related genera. These procedures have given probable evaluations of the direction of evolution for several distinctive features of *Allocapnia.*

Female sternites 7 and 8. Within *Allocapnia* these two sclerites may be either fused (Fig. 52) or separated by a complete membranous strip (Fig. 54). Both conditions occur in several groups; hence from evidence within the genus it is not possible to decide with any degree of certainty which condition is ancestral. In most related genera within the family Capniidae and also in related families, these two sternites are separated by a membranous fold similar to that between the more basal segments of the abdomen. On this basis it would seem that the separated condition of the segments was ancestral, the fused condition specialized or derived.

Dorsal process of male eighth tergite. Within *Allocapnia* this structure varies from an arcuate quadrant (Fig. 12) to a diversity of forms, including cushionlike pads (Fig. 20), bilobed or trilobed transverse structures (Figs. 29, 46), and sinuate, single prolongations (Fig. 35). All of them are heavily sclerotized and almost all are surmounted by fine black crenulations. Nothing exactly like it occurs in related genera, but some species of *Capnia,* especially members of the *nana* complex, have an arcuate dorsal process similar in shape and postion to the dorsal process of *Allocapnia vivipara, malverna,* and their immediate allies. The process in *Capnia* appears much less specialized, being only moderately heavily sclerotized and bearing apical hairs rather than crenulations. It is remarkably suggestive, however, as a possible forerunner of the structure in *Allocapnia* and as an indication that the arcuate process in *Allocapnia* represents the true primitive state of this character.

Dorsal process of male seventh tergite. In *Allocapnia* several groups lack dorsal processes on this segment and most groups in which it occurs have some members that lack it. From evidence within *Allocapnia,* the unadorned seventh tergite would therefore seem to be the ancestral condition for the genus.

If one compares this conclusion with conditions in various groups of *Capnia,* from which *Allocapnia* arose, a paradoxical situation arises. It seems obvious that in the progenitor of *Allocapnia,* the seventh male tergite had a dorsal process but the eighth tergite had none, and that in the lineage leading to *Allocapnia* the genetic expression of this process became transferred from the seventh to the eighth tergite. At this point, and, anticipating the results of the phylogenetic study of *Allocapnia,* it would appear that in at least two lineages this dorsal process appeared again on the seventh tergite. The simplest inference is that in these instances the genetic control for the dorsal process of the eighth tergite became expressed in caricature fashion on the seventh tergite also. After its evolution on the seventh tergite in a caricature or mime condition, the process evolved in various independent ways.

Upper limb of epiproct. In most of the species groups of *Allocapnia* and related groups of *Capnia,* this structure is elbowed well below the apex and the differentiated apical portion is relatively simple, thus suggesting the primitive condition for the genus.

Wings. Within *Allocapnia* the wings vary in length from those which extend beyond the apex of the abdomen (Fig. 1) to minute bractlike structures (Fig. 3). The longer wings have a venation only slightly reduced from that in fully winged species in other stoneflies, whereas the minute wings have no semblance of an insectan-type venation. If the latter were the ancestral type, the former should not have ancestral patterns of venation but rather some venational proliferation of the reduced type. This not being the case, the longer-winged, typically-veined type of wing would certainly appear to be ancestral for *Allocapnia.*

THE ANCESTOR OF *ALLOCAPNIA*

By adding together the primitive conditions of the above characters, the ancestral form of *Allocapnia* (Ancestor 1 in Fig. 86) very likely possessed a male having moderately long wings, eighth tergite not greatly elevated posteriorly and bearing a simple arcuate dorsal process, and a double epiproct in general like that in *malverna;* and a female having a membranous strip on the eighth tergite, and with the seventh and eighth sternites well separated by a membrane. From this ancestor the various groups may be derived in relatively simple steps (Fig. 86).

Evolution of the Species Groups

Ancestor 1 apparently gave rise to two lineages. In the one that evolved into Ancestor 2 and the *vivipara* group, the male changed little, but in the female the seventh and eighth sternites became fused (Fig. 51). In the line leading to Ancestor 3 the female changed little, but in the male the eighth tergite became considerably elevated posteriorly (Fig. 15), with the result that the dorsal process is carried much higher above the general level of the abdomen.

Ancestor 3 gave rise to two lineages. One lineage, leading to Ancestor 4, apparently changed little and evolved into the *recta* group, whose most primitive species *malverna* has a combination of characteristics exactly like those postulated for Ancestor 3. In the second lineage, leading to Ancestor 5, the dorsal process of the male eighth tergite became definitely incised on the meson, forming a bilobed structure (Fig. 29). This bilobed process is typical of at least the primitive species of the remaining groups of the genus. Ancestor 5 gave rise to three lineages. In the one leading to Ancestor 6 the dorsal process of the male eighth tergite became a flattened, cushionlike structure roughly as long as wide (Figs. 20, 21). Ancestor 6 gave rise to two lineages. In the one leading to Ancestor 7 and the *virginiana* group, the female remained simple, but in the male the upper limb of the epiproct became unusually massive (Fig. 20). In the line leading to Ancestor 8, the progenitor of the *granulata* group, the dorsal cushion of the male eighth tergite became divided into two lateral halves (Fig. 21) and the mesal area of the apical margin of the female eighth sternite became differentiated as a wedge-shaped projecting lobe (Fig. 57). In the lineage that arose from Ancestor 3 and evolved into Ancestor 9, the progenitor of the *mystica* group, little change occurred. The third branch of Ancestor 3 led to Ancestor 10 in which the seventh and eighth female sternites became partially fused by a narrow striate area on the meson (Fig. 63). In one line evolving from Ancestor 10, the male seventh tergite evolved a dorsal process (Fig. 30) and the female seventh sternite evolved a differentiated mesal wedge (Fig. 63), resulting in Ancestor 11. This form gave rise to two lineages, one evolving into Ancestor 12, which changed little and is represented now only by the species *illinoensis*, the other leading to Ancestor 13 in which the apex of the upper limb of the epiproct became short and sagittate (Fig. 34), subsequently evolving into the *forbesi* group.

In the second lineage arising from Ancestor 10, the female seventh and eighth sternites became solidly fused and the line of fusion formed a slightly arcuate, heavily sclerotized, sharp ridge and valley (Fig. 72). This is represented by Ancestor 14, which gave rise to two lineages. In the line evolving into Ancestor 15, the basal segment of the upper limb of the epiproct became elongate and the apical segment short (Fig. 38). Ancestor 15 gave rise to two lineages. In the one evolving into Ancestor 16, known only from the species *jeanae*, the dorsal process of the male eighth tergite became high and massive (Fig. 37). In the lineage leading to Ancestor 17, the progenitor of the *rickeri* group, the apical segment of the upper limb of the epiproct became conspicuously knobbed in lateral view (Fig. 38). In the lineage leading to Ancestor 18, the progenitor of the *pygmaea* group, the apical margin of the female eighth sternite became produced into a wide, shining, sclerotized flap that could be deflected inward so that it is often tucked in under the apex of the segment (Fig. 77).

THE *VIVIPARA* GROUP

The *vivipara* group is composed of three species of which the most primitive is *brooksi.* In it the male has well-developed wings, and the center of the female eighth tergite is membranous. From a *brooksi*-like form arose Ancestor 19 in which the male wings became reduced to minute pads (Fig. 3) and the female eighth tergite became entirely sclerotized (Fig. 50A). A species representing this stage is *tennessa.* From Ancestor 19 also arose a line in which the epiproct became greatly elongate, represented by *vivipara* (Fig. 12).

THE *RECTA* GROUP

Because *malverna* is essentially what is postulated as Ancestor 4, there are some grounds for considering that the two lines leading from Ancestor 4 should rather come from Ancestor 3. We are considering the remarkable similarity of *malverna* and *mohri* in many details of the process of the male eighth tergite and the female eighth sternite as evidence that Ancestor 4 was different at least in time from Ancestor 3.

The most primitive species of this group is *malverna* (Fig. 15). In addition to little-changed *malverna,* Ancestor 4 also gave rise to Ancestor 20 in which the long apical segment of the upper limb of the epiproct became wide, thin, flat and armed dorsally with minute sharp spines angled toward the base (Fig. 16); representative of this lineage is *mohri,* which otherwise is remarkably similar to *malverna.* In both species the dorsal process of the male eighth tergite forms a horseshoe-shaped elevated ridge open posteriorly and with a heavily sclerotized floor joining the inside margins of the ridge.

In addition to *mohri,* Ancestor 20 gave rise to Ancestor 21 in which the dorsal process of the male eighth tergite became a solid, buttonlike, small knob, a condition found in *recta* (Fig. 17). From Ancestor 21 a lineage evolved in which the upper limb of the epiproct became narrowed and markedly upturned at the apex, represented by *loshada.* An apparently more recent Ancestor 22 (probably identical to the ancestoral form of *recta*) gave rise to a little-changed lineage represented by *recta* itself and a sister line represented by *polemistis,* in which the knob of the dorsal process of the male eighth tergite became reduced to a smaller anterior projection.

THE *GRANULATA* GROUP

The most primitive member of this group is *fumosa* (Fig. 21), a little-changed offshoot of Ancestor 8. The other branch, leading to Ancestor 23, is a lineage in which the corners of the male eighth tergite evolved into short conical lobes, one beneath each lobe of the dorsal process, giving the entire structure a four-lobed appearance (Fig. 22). From this form arose three lines. The most primitive one led to Ancestor 24, from which arose *warreni* and *unzickeri*. In the second line, known only from *granulata,* the upper limb of the epiproct became more elongate. In the third line, leading to Ancestor 25 and subsequently to *frisoni* and *peltoides,* the process of the male eighth tergite evolved a basal angulation, especially noticeable in profile (Fig. 25).

THE *MYSTICA* GROUP

The three members of this group, *zekia, wrayi* and *mystica,* form a closely knit complex of which *wrayi* is the least derived and is probably remarkably like Ancestor 9. *A. mystica* differs from *wrayi* primarily in the longer upper limb of the epiproct (Fig. 29). Should *zekia* prove to be a distinct species and not a variant of *wrayi,* then both *zekia* and *mystica* would each differ from *wrayi* in one small derived characteristic and on the basis of present information it would be impossible to know in what order these arose from Ancestor 9. In Fig. 86 all three are therefore depicted as a trichotomy.

Ancestor 9 itself poses a problem. On morphological grounds there is no reason to consider it different from Ancestor 5. The remarkable similarity between *mystica, wrayi,* and *zekia,* however, suggests that these three as a unit are not older than the progeny of Ancestors 19, 21, and 22. According to this thinking, used also in differentiating Ancestors 3 and 4 in the *recta* group, we are considering that Ancestor 9 represents a population existing later in time than Ancestor 5.

THE *ILLINOENSIS* GROUP

The rare species *illinoensis* has the female seventh and eighth sternites much like those of the *granulata* group and the *forbesi-ozarkana* branch of the *forbesi* group, especially in regard to the triangular general nature of the mesal area of the eighth sternite and the manner in which its lateral points are made conspicuous by attached membranous areas; as in the other species mentioned, in *illinoensis* also the lateral areas of the eighth sternite are concave and well delineated (Fig. 63).

In *illinoensis* also the mesal part of the membranous connection between the seventh and eighth sternites is slightly sclerotized and slightly transversely striate, highly suggestive of the condition found in *forbesi*, although the posterior edge of the seventh sternite is not produced mesally and rolled under as in species of the *forbesi* group. In the male of *illinoensis*, the upper limb of the epiproct (Fig. 30) is much like that of *mystica* or *granulata*, with no suggestion of the sagittate outline found in most of the species in the *forbesi* group. The male seventh tergite, however, has a dorsal process that is similar to but smaller than that of the eighth tergite. Because of its similarity to the *forbesi* group in the general shape of the female eighth sternite and the process of the male seventh tergite, there is reason for thinking that *illinoensis* is a primitive offshoot of Ancestor 11 which is also the stem of the *forbesi* group.

THE *FORBESI* GROUP

The members of this group, the progeny of Ancestor 13, show a simple progression of derived states and all but *minima* fit into a cohesive arrangement. Ancestor 13 gave rise to two lineages. In one, leading to Ancestor 26, the process on the male seventh tergite remained posterior (Fig. 32), as in *illinoensis*, but the female eighth tergite became sclerotized as in Fig. 50A. In the other lineage, leading to Ancestor 27, the process on the male seventh tergite moved anteriorly (Fig. 33), whereas the female changed little.

Ancestor 26 evolved into two species, little-changed *ozarkana* and *forbesi*, in which the process on the male seventh tergite became a high, undivided cone.

Ancestor 27 gave rise to *curiosa*, in which the male tergites became highly ornamented (Fig. 36) and the apical extension of the female seventh sternite became much produced (Fig. 69), and to Ancestor 28, in which the center of the female eighth sternite became a rectanguloid flat area extending the whole length of the segment (Fig. 66). Ancestor 28 in turn gave rise to little-changed *pechumani* (Fig. 33) and to *maria*, in which both the dorsal process of the male eighth tergite (Fig. 34) and the flat part of the female eighth sternite (Fig. 67) became narrower.

The species *minima* is atypical of the group in that it lacks a dorsal process on the male seventh tergite, the dorsal process of the eighth is high, narrow, and uncleft, and the apical segment of the upper arm of the epiproct is small and poorly differentiated (Fig. 35). A definite clue to its relationship is that *minima* (Fig. 68) has a female almost exactly like that of *maria* and would therefore appear to be a branch of the *maria* lineage in which the process of the male seventh tergite has become lost and that of the male eighth tergite has become even longer and narrower than in *maria,* and in so doing has lost its cleft.

THE *JEANAE* GROUP

In general characteristics of the male genitalia (Fig. 37), *jeanae* bears much resemblance to the *mystica* group. The female characters (Fig. 70) suggest a close tie with the *zola* complex of the *rickeri* group. Such a combination suggests that *jeanae* is a primitive offshoot of Ancestor 15, which is also the progenitor of the *rickeri* group. In *jeanae* the basal segment of the upper arm of the epiproct is elongate, as is typical of the *rickeri* group, and this condition would therefore seem to have been typical of Ancestor 15 also.

THE *RICKERI* GROUP

The six species comprising this group form two well-marked complexes of three species each. In *cunninghami, zola,* and *perplexa,* the female seventh and eighth sternites are fused, and the line of fusion forms a sharp, heavily sclerotized arcuate ridge (Fig. 75). In *sandersoni, rickeri,* and about 50 percent of *stannardi,* the same two sternites have no ridge across the line of fusion with the result that the two sclerites appear to flow together evenly along the meson (Fig. 73). The latter condition would appear to be the derived one. It is a unique structure known otherwise only in the *vivipara* group.

From this it appears that Ancestor 17 gave rise to Ancestor 29, in which the female lost the distinctive crease between the seventh and eighth segments (Fig. 73), and to at least one additional lineage, the latter including some combination of *zola, cunninghami,* and *perplexa.* To date we have found no derived character combining these three into a distinctive group. Further, the three are so remarkably different from each other that no recency of origin can be claimed on unusual morphological similarity. The only logical course is to consider each of these three species as representing a separate line arising from Ancestor 17.

The peculiarities of *zola* (Fig. 42) and *perplexa* (Fig. 43) rest in the unusual shape of their structures. In the case of *cunninghami* (Fig. 39), another factor enters. Although in other characters a typical member of the *rickeri* group, *cunninghami* has a three-pointed dorsal process on the male eighth tergite almost exactly like that of *nivicola*

(Fig. 49); in addition the seventh tergite has a similar small process in both species. This combination of highly derived characters of two separate lineages occurring in one species suggests strongly that *cunninghami* is of hybrid origin. One presumed parent would have been a species much like Ancestor 17, the other would have been a *nivicola*-like species, possibly resembling Ancestor 34.

Ancestor 29 gave rise to *sandersoni* (Fig. 38), its most primitive derivative, and to Ancestor 30 in which the lobes of the dorsal process of the male eighth tergite became far apart (Fig. 40). The latter subsequently evolved into *rickeri* and *stannardi.*

THE *PYGMAEA* GROUP

The basic evolution of this group, Ancestor 18, and its progeny is indicated by a phenocline of the dorsal process of the male eighth tergite from a relatively narrow bilobed structure in *pygmaea* (Fig. 44) to a wider one in *aurora* (Fig. 45) to a tridentate one in the other four species (e.g., *ohioensis,* Fig. 46). This phenocline is more or less paralleled by the apical flap of the female eighth sternite (Figs. 77-83). Because the *pygmaea* dorsal process is only slightly different from that in more primitive *mystica* (as in Ancestor 5), this end of the phenocline would represent the ancestral condition. With this point as a base, a highly probable phylogenetic tree of the group can be constructed.

Ancestor 18 gave rise to a little-changed line evolving into *pymgaea* and a second with a wider dorsal process leading to Ancestor 32. The latter gave rise to *aurora* (Fig. 45) and to a line having a tridentate dorsal process (Fig. 46), Ancestor 33. In *ohioensis* and *indianae* the male seventh tergite also has a tridentate process that is a diminutive form of that on the eighth (Figs. 46, 47); in *smithi* and *nivicola* the seventh tergite has a small, untoothed process (Figs. 48, 49). The question is: which of the two conditions of the seventh tergal process is ancestral? It seems to us more reasonable to think that the tridentate form is, because this could have arisen as a single homeotic mutant and later have been modified in subsequent lineages.

With this explanation, Ancestor 33 would have been almost like its daughter line *ohioensis* and would have given rise also to the derived line producing *indianae* and to Ancestor 34, in which the dorsal process of the male seventh tergite became vestigial. This latter gave rise to *smithi,* in which the male dorsal process of the eighth tergite became modified (Fig. 48) and to *nivicola,* in which the female eighth sternite became modified (Fig. 83).

GEOGRAPHIC DISPERSAL

The original stimulus for beginning this study of *Allocapnia* came from an observation that *Allocapnia pygmaea* was primarily a subboreal northern and eastern species but had a thriving population in the Missouri Ozarks far removed from the remainder of the species' range. This circumstance suggested either unusual powers of dispersal or a relict distribution possibly associated with Pleistocene events.

Vagility

All *Allocapnia* males are flightless, but because *Allocapnia* species have at least some apparently fully-winged females in most populations, their vagility, or ability to disperse, would seem to be normal. A closer examination of *Allocapnia* females raises substantial doubts about this conclusion. In the females the wings are never so long as in fully-winged close relatives, always have a degenerate venation, and the thoracic sclerites associated with flight muscles are reduced. These features suggest strongly a long-term relaxation of the selection pressures associated with free flight.

Subsequent observation has confirmed this view. We have seen startled winged females plane downward from bridges, but have never seen one in true sustained flight. Usually when startled both sexes simply drop. High vagility does not, therefore, appear acceptable as an explanation of long gaps in ranges.

A glance at the ranges of *granulata* (Fig. 94), *minima* (Fig. 100), and other widespread species demonstrates that at least some species of the genus have been able to disperse long distances. We have evidence that downstream transport of gravid females is fairly common, with catches of brook-species females occurring in large streams 20 and 30 miles downstream from the point of breeding. In northern areas we have observed *Allocapnia* adults on ice blocks being carried downstream; this mechanism could conceivably transport large numbers of individuals for hundreds of miles.

Such transport provides an explanation for females getting from the mouth of one stream to that of another, but not for the dispersal up the new stream necessary for establishing a new colony. This is no real problem because both sexes wander freely over snow, ice, or the ground up to at least a hundred yards. In 17 years they could travel a mile.

These activities do not explain the movement of species in a general upstream dispersal of large watersheds, which has certainly occurred. The only explanation we have is the climbing and planing habit of *Allocapnia*. Adult females are known to climb to bridge railings at least a hundred feet above a stream and to climb trees or houses situated several hundred feet from a stream bank. Planing of the females from these high perches might account for the slow movement of a population along a series of habitable watercourses either toward the upper or lower part of a watershed. With the vagility of *Allocapnia* species established as relatively low, large discontinuities in range would appear to indicate past dispersals across terrain that was formerly favorable but is now unfavorable to the success of the species involved. Exceptions would include only instances in which extensive downstream transport offered a satisfactory explanation.

Association with Pleistocene Events

To aid in visualizing possible Pleistocene associations of *Allocapnia* species, the distributions of these species have been plotted on base maps showing the known maximum limit of the Pleistocene glaciations, with special emphasis on the most recent one, the Wisconsinan (Figs. 88-109).

Dispersal Patterns of Species Groups

The next step in the investigation rests on plotting present distributions and comparing these with the phylogeny of the genus, depicted in Fig. 86, together with the numbered hypothetical ancestors referred to in this section.

When examining the distribution of any one species or species group, its relation to the total distribution of *Allocapnia* can be seen by comparing it with Figs. 87, 99, and 100. These show all localities from which the genus has been obtained. We have not included negative collections, but have many extending west to the Black Hills of South Dakota and south to Florida and south-central Texas. Undoubtedly we have missed many significant populations and some species, and we welcome additional information.

THE *VIVIPARA* GROUP (Fig. 88)

Two circumstances of the *vivipara* group suggest its ecological evolution. The most primitive member, *brooksi*, inhabits clear, cold, fast streams, and the more specialized pair *tennessa-vivipara* inhabits smaller streams and has a marked tolerance of barnyard pollution. The simplest explanation is that Ancestors 2 and 19 were eastern, Ancestor 19 becoming adapted to warmer and slower streams, and that subsequently Ancestor 19 split into a northern and a southern population west of the Appalachians, the former evolving into *vivipara*, the latter into *tennessa*.

The sharp boundary without overlap between *tennessa* and *vivipara* suggests strongly that the two occupy the same ecological niche and are mutually exclusive, the latter replacing *tennessa* where it has an ecological advantage. Where *vivipara* occurred before the Wisconsinan we do not know, but presumably at the onset of this period it moved southwestward into the Cumberland Plateau and Cincinnati Arch areas and occupied what is now the southern part of its range. It is possible that in pre-Wisconsinan times *tennessa* occurred further north and its range was restricted by competition with *vivipara*.

Postglacially *vivipara* fanned out northward. The uniformity of its variation pattern throughout its present range indicates that this entire dispersal arose from a contiguous and restricted population.

THE *RECTA* GROUP (Figs. 89, 90)

Of the five species in the *recta* group, only *recta* extends into previously glaciated terrain. It would therefore appear that most of its evolution occurred well south of the area occupied by the Pleistocene glaciers. Because the two primitive members, *malverna* and *mohri,* occur in the Ozark-Ouachita area, it is reasonable to suppose that Ancestors 4 and 20 occurred there also, and that Ancestor 21 represents a dispersal from this area to the more eastern montane or hill areas. Here *recta, polemistis,* and *loshada* speciated. The very local *polemistis* probably evolved in the Black Warrior uplift of northwestern Alabama where it now resides. The isolation locale of *recta* and *loshada* cannot be determined, but could well have been along the western flanks of the Appalachians.

Whatever these areas, all five species of the group must have been south of the glacial border through Wisconsinan time, and in post-Wisconsinan time only *recta* dispersed north into previously glaciated areas.

Variations within *recta* add one other point to our understanding of geographic movements of the group. The ancestral form (Fig. 90) is rigidly restricted to southern Alabama, but, in all collections taken to date, occurs in hybrid swarms containing both the ancestral and derived forms and their intergrades, in various proportions (Table).

PROPORTIONS OF ANCESTRAL, DERIVED, AND HYBRID FORMS OF *ALLOCAPNIA RECTA* IN ALABAMA

ALABAMA COUNTY	ANCESTRAL FORM	HYBRID FORM	DERIVED FORM
	Isolated southern population of *A. recta*—n = 771		
Butler	2	4	1
Choctaw	0	2	0
Clark	21	13	8
Conecuh	226	176	300
Escambia	1	9	3
Monroe	0	1	4
TOTALS	250	205	316
PERCENT	32	27	41
	Closest part of northern range—n = 517		
Lee	0	2	59
Russell	1	3	300
Jackson	0	0	40
Calhoun	0	0	80
Elmore	0	0	6
Coosa	0	0	26
TOTALS	1	5	511
PERCENT	t	1	99

In the isolated southern area the ancestral form may reach 50 percent of the population. The only occurrence of the ancestral form in the contiguous part of the more northern range is one specimen and three intergrades in a population of 300 individuals of the derived form. This is the form occuring throughout the remainder of the range.

This distribution of the ancestral form of *recta* leads to the following reconstruction (Fig. 91):

1. Originally the ancestral form of *recta* occurred in the southern Appalachians and either by downstream transport or during a wetter and cooler climate dispersed into the hilly area in extreme southwestern Alabama.
2. Contact between this southwestern population and the northern part of the range was effectively broken, possibly during a drier period.
3. The southwestern ancestral population changed little; the northern population evolved into the derived form of *recta*.
4. At some subsequent time derived *recta* dispersed from the north into ancestral territory and hybridized with the ancestral form.
5. Later a distributional discontinuity reappeared, leaving a negligible number of ancestral individuals to the north (only one ancestral and three hybrids of 300 individuals collected to date), and with a proportion of collected individuals in the ancestral territory of 316 derived, 205 hybrids, and 250 ancestral. If the sorting of the parent types was correct and if the two forms represented simple alleles with incomplete dominance, the hybrid figure should be over 550. There is therefore a selection against the hybrids or the genetic picture is more complex. It is difficult to make a choice with the limited data at hand.

The area occuppied by the ancestral form has numerous small streams issuing from caves. These streams are undoubtedly of early geographic origin and account for the persistence of the ecological features of the area conducive to *Allocapnia* survival. Here also occurs the local endemic and peculiar salamander *Phaeognathus hubrichti* Highton.

THE *VIRGINIANA* GROUP (Fig. 92)

The range of *virginiana,* the only species in this group, gives no indication of its past geographic history. The fact that it is eastern and a daughter lineage of Ancestor 6 is useful in figuring out the dispersal of the *granulata* group.

THE *GRANULATA* GROUP (Figs. 93, 94)

Of the six species comprising the *granulata* group, the progeny of Ancestor 8 (Fig. 86), the most primitive is the Great Smoky Mountain species *fumosa*. The remainder comprise two pairs of two sister species each, all four with small ranges, and the widespread species *granulata*.

The two pairs of sister species are remarkably alike geographically. In one pair, *frisoni* is known only from the area immediately west of the Appalachians and *peltoides* occurs only in the Ozark-Ouachitas. In the other pair, *unzickeri* is a local endemic centered in the more southern part of the Cumberland Plateau and *warreni* is known only from the Arkansas Ozarks. It is obvious that the immediate progenitor of each pair (Ancestors 24 and 25) dispersed between these areas, and that later its range contracted so as to produce isolated eastern and western populations, each of which evolved into a distinctive species. From this information it is impossible to know in which area the two progenitors originated; on this basis alone each progenitor could have arisen in either area.

The widespread species *granulata* offers considerable evidence that it was of eastern origin (Ross and Yamamoto, 1967), because the eastern morphological types appear to be the more ancestral. This view, plus the eastern distribution of *virginiana* and *fumosa*, leads to the conclusion that the entire group evolved in the Cumberland Plateau–western Appalachian region, and that subsequently Ancestors 24 and 25 and an early stage of *granulata* dispersed from there into the Ozarks. Because *warreni* and *peltoides,* and possibly *unzickeri* also, owe their persistence to local spring-fed streams cooler in summer than surface-water streams, presumably the dispersals of Ancestors 24 and 25 occurred when conditions between the present ranges were generally cooler and wetter than at present, but dating these movements is difficult.

As with *recta,* the species *granulata* exhibits intraspecific variation (Fig. 84) correlated with distribution (Ross and Yamamoto, 1967), but it is more complex than that in *recta.* It has resulted in the four populations outlined on pages 29-30, together with the various ancestral steps implicit in their evolution. The following sequence of events seems necessary to explain these populations:

1. Originally *granulata* occurred along the western flanks of the Appalachians in larger streams than its congeners in the area.
2. Warmer and drier conditions caused a break in its range, resulting in a population in the southern Appalachian area isolated from a more northern one.

3. In the southern population (Population 1), little change occurred; in the northern population (Population 2), the wings became shorter and the ecological tolerance shifted to warmer and slower streams.

4. Cooler and wetter conditions (the onset of the Wisconsinan glaciation?) resulted in Population 2 being displaced both southward and westward. Southward it came into contact with Population 1 and merged with it in areas where their ecological interfaces met. Westward it dispersed to a greater degree than any other *Allocapnia,* reaching the Wichita Mountains of south-central Oklahoma.

5. Drier (and/or warmer) conditions caused a shrinkage of its westernmost colonizations. The best explanations of its present NE-SW transect calls for an initial break along the Mississippi River area. After this the eastern population remained typical of Population 2, but the western population moved toward Population 3. Continued dry or drier conditions brought about a cleavage of the western portion of the range into Population 3, restricted to the Ozark-Ouachita Mountains, and Population 4, isolated in the Wichitas. In Population 3 the male genitalia became further derived, in Population 4 the wings became extremely reduced. Both populations were undoubtedly restricted to areas in which only artesian streams provided suitable habitats for survival.

6. Subsequent wetter conditions again resulted in streams fed by only surface water in which the species could survive. Such conditions would have caused a meeting of Populations 2 and 3 in Illinois and Missouri. There is an indication that the southwestern portion of Population 2 extended westward into central Louisiana and that some individuals of Population 3 moved south into the same area. This would explain the populations in the Arbuckle Mountains of Oklahoma intermediate between Populations 3 and 4, and the population from Louisiana, Missouri, that is intermediate between Populations 2 and 3.

7. Drier and/or warmer conditions associated with the dissipation of the Wisconsinan ice lobes resulted in the reisolation of Populations 3 and 4 and the dispersal of Population 2 northward on all fronts.

Through all this, Population 1 may have moved very little.

These events are depicted diagrammatically in Fig. 95.

THE *MYSTICA* GROUP (Fig. 96)

The *mystica* group, the progeny of Ancestor 9, has all the attributes of an archaic one. Often the surviving members of archaic lineages present a tangled web of evidence difficult to unravel, but the *mystica* group seems to be a cohesive, simple picture. In addition to the enigmatic *zekia*, known only from a single specimen, the group comprises two closely related species, *wrayi* to the east and *mystica* to the west of the central and southern Appalachians, both occurring in moderately warm small streams. The occurrence of two hybrid populations near the interface of the two indicates that relatively recently there has been some dispersal of *wrayi* westward through some of the lower passes.

If *zekia* is a distinct species, two evolutionary possibilities are indicated. One assumes that Ancestor 9 (a form probably identical with *wrayi*) occurred originally in the Piedmont around the southern end of the Appalachians, and that at a later time the range of Ancestor 9 moved northward on both sides of the mountains and became divided by them into two isolated populations. The eastern population evolved into *wrayi*, the western into *mystica;* later a local isolated population of *wrayi* evolved into *zekia*.

The second possibility is that Ancestor 9 was originally east of the mountains and that (1) during a period of cooling climates its range was displaced southward, leaving an isolated northern population in a local warmer pocket, this isolate evolving into *zekia;* and (2) during a warmer period migrants dispersed through the lower mountain passes or around the southern end of the chain, establishing a colony that eventually became *mystica*.

If *zekia* is not a distinct species, then either of the above explanations would be applicable for the origin of *wrayi* and *mystica* from Ancestor 9. Because *mystica* occurs widely in the Ozark-Ouachita area, there is the possibility that this later was the original home of *mystica*, and that Ancestor 9 first divided into an Appalachian and an Ozark dichotomy. It is difficult to choose between these most likely alternatives. Whichever explanation is correct, in post-Wisconsinan time *mystica* dispersed widely but only slightly into previously glaciated terrain.

THE *ILLINOENSIS* GROUP (Fig. 97)

With only one species known, it is difficult to deduce much about the ancestry of the *illinoensis* group. Considered in relation to the next group, *illinoensis* was probably a northern subboreal species whose range was displaced southward during the Wisconsinan, and which colonized the deglaciated areas during post-Wisconsinan time. The probable route of this colonization is of interest. The Illinois populations, occurring in rocky streams in two deep, shaded ravines, differ slightly and modally from the others, offering evidence that the Wisconsin population arrived there via the route indicated in Fig. **97**. The colonists moving north through the Illinois route were apparently unable to cross the flat glaciated terrain of northern Illinois, Indiana, and Ohio.

THE *FORBESI* GROUP (Figs. 98-100)

The total ranges of this group, the progeny of Ancestor 13, are on the whole more northern than the preceding groups. The dispersal patterns have points that are most easily seen by first treating the progeny of Ancestors **26** and **27** separately. Ancestor **26** (Fig. **98**) evidently dispersed between the Cincinnati Arch area and the Ozarks, and became divided into two isolates. Subsequently the Ozark population evolved into *ozarkana* and the more eastern into *forbesi*. The original home of Ancestor **26** could have been in either place; the more primitive condition of *ozarkana* suggests the Ozarks.

Ancestor **27** was almost certainly a northeastern species. The distributional and ecological nature of its progeny are best explained by its initial disruption into a southern Appalachian isolate and a northern Appalachian one. The former apparently evolved into *curiosa*, the latter into Ancestor **28**. Present-day distribution patterns favor this development, even if abstrusely. Except for enigmatic *minima*, discussed later, the situation is highly probable. If one assumes that Ancestor **27** originally extended along the Appalachian ridge, then during a period of lower rainfall and/or higher temperatures it became divided into two isolates, one in the southern Appalachians, the other in the northern Appalachians. The southern isolate evolved into *curiosa* with its peculiar morphological features and also with a dependence on small rapid mountain streams. This dependence would be completely understandable if *curiosa* evolved in an isolated montane area during a generally warm cycle of continental climates; that is, during an interglacial period.

The northern isolate, Ancestor **28**, apparently changed little, remaining as a clear-brook or small-creek species. At a later time Ancestor **28** split into two populations, possibly also northern and southern, or perhaps eastern and western on either side of the Appalachians (Fig. **99**). The more northern or western population evolved into *pechumani*, the more southern or eastern one into the more derived *maria*.

The time of geographic fission of Ancestors **27** and **28** is open to question, as is also the area they occupied during the Wisconsinan glaciation. Presumably *curiosa* occurred along the flanks of the Appalachians in roughly the southern part of its present range. The glacial range of *pechumani* had to be south of its present one, which is entirely within glaciated terrain.

Because the ranges of *pechumani* and *maria* overlap only little now, it is likely that they were separate during the Wisconsinan, one on each side of the Appalachians south of their present ranges. The hybridization pattern adds another bit of evidence. The ranges of these two species overlap to some extent to the south with no sign of hybridizing; they touch to the north with evidence of considerable hybridizing. These circumstances suggest that (1) the two species had already differentiated before the Wisconsinan, (2) during the Wisconsinan they occupied contiguous ranges and the populations in immediate contact evolved complete sexual isolation, (3) the post-Wisconsinan northeastern dispersal of both species was made by peripheral populations that had not been in interspecific contact, (4) *maria* dispersed on the Atlantic side of the northern uplands, *pechumani* on the northwestern side, and (5) when the two species came into contact north of the higher uplands in New Brunswick, their populations were probably genetically distinct but not sexually isolated.

TACHYTELY IN *A. MINIMA*

The evolution and dispersal of *minima* is enigmatic in several regards. First, it is much smaller than any other *Allocapnia*, so much so that the females can probably fly almost normally. Second, its reduced male tergal processes and apices of the epiproct limbs plus the remarkable similarity of its female to that of *maria* suggests something peculiar in either its mode or speed of evolution. Third, it apparently arose from a brook-inhabiting lineage and evolved into a large, fast-stream species. Fourth, it is the only species of the genus occurring in Newfoundland. Fifth, it is the only member of the genus occurring north to the tundra line (Fig. 100).

The female characters indicate that *minima* evolved comparatively recently from a *maria*-like ancestor. The male structures and ecological information are evidence of a drastic change in the lineage, sufficient to come under Simpson's (1944) definition of tachytely, or unexpectedly rapid evolution. An evolutionary change producing both radical and rapid change calls for unusual genetic change combined with strong selection pressures acting on this change. The most likely circumstances in which both factors would come into play involve hybridization and restriction to a rapidly changing environment.

The possibility of hybridization occurring in the progeny of Ancestor 28 is excellent. Its two daughter species *maria* and *pechumani* hybridize now and would have done so if they had come into contact previously.

Restriction to a rapidly changing environment could readily have occurred on Newfoundland. The possibility that *minima* survived the Wisconsinan only on that island was first suggested by McAlpine (Ross et al., 1967), but, not at that time knowing of the northern Quebec record near tree line, his coauthors outvoted him. His deduction now seems to be an excellent possibility. We do not know the ranges of *pechumani, maria,* or other species during the Sangamon interglacial period preceding the Wisconsinan glaciation, but they could have occurred at least slightly north of their present range. This would have resulted in distributions along the north side of the Gulf of St. Lawrence and on Newfoundland. When the Wisconsinan glacier advanced over most of Newfoundland, any *Allocapnia* would have been trapped on its southeastern Avalon Peninsula.

The previous opinion (Ross et al., 1967) concerning *Allocapnia* survival on this Peninsula therefore needs revising. Information given by Jenness (1960) indicates a tundra or high-latitude boreal forest cover, but in all probability with willow or birch along the watercourses, much like the area from which *minima,* but only *minima,* is now found (Brown, 1965). If two or more species of *Allocapnia* had been isolated on the Avalon Peninsula, cooling conditions could have gradually reduced their numbers to a low point at which interspecific stress matings might have increased to produce a heterogeneous hybrid swarm. Such a genetically labile population would have been the most likely basis for the original peculiar combinations of morphological and correlated ecological characteristics. Perhaps this is how *minima* arose.

Another possible explanation for the origin of *minima* involves the model set forth by Wynne-Edwards (1937) concerning the local endemic plant species reported by Fernald (1925) for the Gaspé Peninsula and other areas of southern Quebec and Newfoundland. Fernald believed that these endemics had survived the Wisconsinan in or near the areas where they still occur, indicating the existence of ice-free areas in the region throughout the last Ice Age. Wynne-Edwards believed that the endemics in question were probably hybrid species resulting from crosses between new arrivals in deglaciated areas during post-Wisconsinan time. Similar postglacial hybridization between species of *Allocapnia* could have set the stage for the evolution of *minima* at almost any time, especially in the northeast.

These are of course only two of many possibilities that can be suggested for the evolution of *minima.* The species could have evolved earlier, before the Wisconsinan, as a sister species of *maria* through ordinary range division of a parental form and gradual slow change in isolation. If the two species are so old, it is curious that they still hybridize. If they were of an older age, during the Wisconsinan *minima* could have occupied an area in the Appalachians south of the glacial front and it would not be necessary to invoke a Newfoundland origin or other unusual circumstances.

THE *JEANAE* GROUP (Fig. 101)

Little can be said about the origin of the single species *jeanae* comprising this group. Indications of both distribution and phylogeny suggest an Ozark lineage of considerable age that is now a geographic endemic.

THE *RICKERI* GROUP (Figs. 102, 103)

In this assemblage of six species, the progeny of Ancestor 17, *sandersoni* is the only local endemic that occurs in the Ozarks. The widespread *rickeri* also occurs there. Only two species, *rickeri* and *zola,* have dispersed northward into previously glaciated areas.

Reconstructing possible dispersal patterns, it is obvious that *cunninghami, perplexa, zola,* and *stannardi* are associated with the Cincinnati Arch and Appalachian area. All four of these species require cold, spring-fed or mountain streams, as does *sandersoni. A. stannardi* is restricted rigidly to the small cascades in the Great Smoky Mountains. This and its close similarity with *rickeri* suggest that they both evolved from an Appalachian form (Ancestor 30) that became divided into a high-mountain southern Appalachian isolate and a low-mountain northern Appalachian one, the latter evolving into *rickeri,* the former into *stannardi.* If this were true, then Ancestor 29 would have originated along the western flanks of the Appalachians and dispersed into the Ozarks, the populations in the two areas soon being isolated. The Ozark isolate evolved into *sandersoni,* the Appalachian isolate into Ancestor 30.

The species *rickeri* evolved an ecological tolerance much broader than any other member of the group, evidenced by the wide variety of streams it inhabits and its wide distribution. Morphologically it is unusually constant throughout its range, suggesting that during the Wisconsinan it probably occupied a relatively small range in the southern Appalachians. From there it spread in late Wisconsinan time northward into New York and Ontario and westward into the Ozark-Ouachitas and from the Ozarks into Wisconsin.

We have made special efforts to document this latter northern leg of *rickeri*'s journey. The populations in Iowa, Minnesota, and Wisconsin are found in sheltered ravines supporting spring-fed streams, as are the more northern Illinois records. A gap in the known occurrences between the extreme northern and west-central Illinois records suggests a natural discontinuity in the range. Between these two points, however, there is a nicely spaced scattering of streams issuing from the Mississippi River bluffs that formerly would have been excellent habitats for *rickeri,* but which are now laden with organic pollution to which *rickeri* is exceedingly sensitive. It therefore appears that this discontinuity is man-made.

In post-Wisconsinan time *zola* dispersed northeastward into New Brunswick. It presumably spent the Wisconsinan period in the southern part of its present range.

This explanation of the dispersal of the *rickeri* group follows Occam's razor in requiring the fewest assumptions in accounting for observed data.

THE *PYGMAEA* GROUP (Figs. 104-109)

An analysis of dispersal paths cannot be made directly from present distribution patterns because several of the six species of this group, the progeny of Ancestor 18, have overlapping ranges. It is therefore necessary to base conclusions on the inferred distribution of ancestral forms. If we consider the progeny of Ancestor 33, three of the species occur around the Cincinnati Arch area and only the highly derived *nivicola* is widespread. Ancestor 33 is thus indicated as a karst-country species living somewhere west of the Appalachians. Its nearest ally, *aurora,* is primarily a southern Appalachian species possibly indicating that at some past time Ancestor 32 occupied a generally southern Appalachian territory. The most primitive species, *pygmaea,* is the only subboreal member of the group. From this it appears that Ancestor 18 was an eastern species that gave rise to a more northern segregate, which evolved into *pygmaea* and a more southern one evolving into Ancestor 32.

In post-Wisconsinan time, only *pygmaea* dispersed extensively northward into deglaciated area. Restricted to moderately large, rapid streams, its present distribution (Fig. 104) stretches across the north with a string of southeastern localities down the Appalachians and the

Cumberland Plateau, and an isolated area in the Missouri Ozarks. The latter raises two questions: How did *pygmaea* reach the north after deglaciation? And how did *pygmaea* reach Missouri?

Evidence for its northward dispersal is provided by morphological variation. The Missouri populations are modally slightly different from all the others as a unit. On this indication one may assume that two populations of *pygmaea* existed during the Wisconsinan maximum, one in Missouri, the other somewhere in the Cumberland Plateau area. The morphological similarity between the latter and the present northern populations makes it simpler to explain the northward spread of the species as a fountainlike dispersal from the more eastern population.

The colonization of Missouri can be explained on paleoclimatic grounds. Today *pygmaea* is restricted in Missouri to cold, large streams issuing from enormous springs, a unique feature of the region. No similar streams are known either between the Ozarks and the Wisconsin localities where *pygmaea* occurs, or the Ozarks and the Cumberland Plateau. These disjunctions appear natural. When the Wisconsinan glaciation began it was undoubtedly fed by greater rainfall than we have at present, at a time when decreasing temperatures were displacing boreal species southward. It is probable that streams between both the Ozarks and Wisconsin or the Ozarks and the Cumberland Plateau were markedly larger, faster, and colder than those of the present. This condition would have provided an avenue for the movement of *pygmaea* into the Ozarks possibly from either direction. It is a curious fact that, except for *pygmaea,* no species of its group occurs west of southeastern Illinois. The lack of large spring-fed streams across some 50 miles of the Illinois Ozarks appears to be a complete barrier to the westward dispersal of *ohioensis, indianae, smithi,* and *nivicola.* If it had been otherwise in the past, surely some relicts of these groups would parallel westward dispersals of *rickeri* and certain other species of *Allocapnia.* Because *pygmaea* requires both larger and cooler streams than these four, it also likely did not disperse westward across the Illinois Ozarks.

We are left with the conclusion that *pygmaea* moved into the Missouri Ozarks by successive southward colonizations of swift laterals of the Mississippi River or allied drainages during the pluvial period at the onset of the Wisconsinan glaciation, but that in the subsequent drier period accompanying deglaciation the same streams that earlier provided a southern passage had shrunk or warmed to the point that they did not provide a northward avenue of dispersal.

The remarks just made concerning the westwardly restricted ranges of *aurora, ohioensis, indianae,* and *smithi,* coupled with the small northward extension of any of them into deglaciated areas (Figs. 105-108), suggest that these four species have inhabited their present general area of distribution through and probably before the Wisconsinan. During warmer or drier climatic periods they would have been more restricted to those areas having the greater discharge of artesian water, during the cooler periods to areas somewhat south of the present ranges. On the basis of topography, however, it seems unlikely that *ohioensis* and *indianae* would have ever extended to the present limits of *nivicola* (Fig. 109).

The relatively recently evolved species, *nivicola,* was also the most northern pre-Wisconsinan member of the brook species of the *pygmaea* group. This is evidenced partially by its present distribution, but more graphically by a series of populations in Kentucky, Tennessee, and West Virginia (marked with an "x" in Fig. 105) that exhibit evidence of hybridization with *aurora.* This hybrid evidence is in an area northwest of known existing populations of *aurora.* It suggests that in pre-Wisconsin times *aurora* occurred north of its present range and *nivicola* north of that; during the early stages of the Wisconsinan, populations of *nivicola* became established southward into the range of *aurora* and some hybridization occurred. Later the contact populations of *aurora* disappeared and the ranges of the two species became separate. The hybridization was slight enough that only minor evidences of it now persist in the two species.

Aside from the hybrid populations mentioned, *nivicola* is remarkably uniform morphologically throughout its range. The best explanation is that during the Wisconsinan *nivicola* occupied a continuous range near its present southern limits and in post-Wisconsinan time dispersed into its present territory.

Early Ancestral Types

Reviewing the probable dispersals for all groups of *Allocapnia,* it seems likely that the entire sequence of ancestral types evolved in the Appalachian system, including its companion ridges and mountainous or hilly country to the northeast.

There is good evidence that Ancestor 3 dispersed from the eastern montane area to the Ozark-Ouachita area in Missouri and Arkansas, and that later Ancestor 15 did likewise. The other basic ancestors (1, 5, 6, 10, 11, 14, 15, and 18) appear to have been strictly eastern.

DISPERSALS AND TIME

It is evident from the foregoing discussion that the present *Allocapnia* fauna is the result of a considerable number of dispersals occurring at different times and places in the past. The post-Wisconsinan dispersals into previously glaciated terrain are obviously time-correlated to the period when the dissipated glaciers made the areas ecologically available. All other *Allocapnia* dispersals must be inferred more indirectly. Unfortunately, there is no fossil record, thus precluding certain useful types of inferences.

To make any progress correlating the history of *Allocapnia* with time, we must rely heavily on the comparative ecology of the species, indications of dispersals adduced from phylogeny and distribution, and geologic evidence that might offer clues as to past ecological conditions in the areas now or previously occupied by *Allocapnia*.

Comparative Ecology

On the basis of stream requirements, the species of *Allocapnia* fall into a small number of ecological groups:

1. Those occupying medium-size, clear, fast streams or small rivers. Includes only *minima* and *pygmaea*.

2. Those occupying larger streams and small rivers, but tolerating slower currents and some turbidity. Includes only *granulata* and *vivipara*.
3. Those occupying smaller streams and tolerating considerable amounts of organic pollution. Includes only *vivipara*.
4. Those occupying small, clear, rapid streams with a gravel or rock bottom. Includes the other 34 species.

These stream requirements of *Allocapnia,* correlated with topography, have resulted in several peculiar distributional features having a significant effect on dispersal opportunities.

MIDWESTERN FLATLANDS

In the glaciated areas of Ohio, Indiana, Illinois, Missouri, and Kansas, the streams are for the most part sluggish and muddy. They flow through very fine glacial alluvium that is carried in suspension for a considerable time. Such streams do not support any species of *Allocapnia.* In some peripheral areas having springs emerging from subterranean strata and flowing for short distances over a rocky or gravel bottom, *Allocapnia* are found in abundance. In general, these flatlands have obstructed the northward dispersal of most species of *Allocapnia* across them. *A. mystica,* for example, has dispersed up river valley systems having deeply eroded ravines with small streams running over exposed rocks, but has not penetrated beyond the southern edge of the flatlands (Fig. 96). The same is true of *recta* (Fig. 90), *indianae* (Fig. 107), and many others. Eastward the terrain was not flattened, resulting in an abundance of clear rocky streams of many types.

Only three species of *Allocapnia* (*granulata, vivipara,* and *rickeri*) appear to have moved northward through the flatlands. The two species *granulata* and *vivipara* thrive in many streams, but only in stretches running through moraines and having a gravel bottom.

In the areas of Illinois and Missouri covered by till of the Illinoian glaciation, even these two species are virtually absent. During periods of greater rainfall when stream currents would be maintained at a higher speed of flow throughout the year, it is likely that stream bottoms through this area would have had more stretches washed clear of mud and have gravel bottoms. Under these circumstances, *granulata* and *vivipara* could have occurred through this area.

As explained concerning the dispersal of *rickeri,* there was probably a series of small, clear, rocky streams along the Mississippi River that afforded an avenue of dispersal through the flatlands for certain clear-stream species of *Allocapnia.*

MISSISSIPPI EMBAYMENT

The Coastal Plain of the southern and eastern United States is almost devoid of *Allocapnia.* The only known exceptions are certain hilly areas having spring-fed streams, including the Jackson Dome area and the area north of it in Mississippi; the Monroe Uplift and associated hill country of southern Arkansas, northern Louisiana, and nearby Texas; and the Conecuh County cave area in southern Alabama. In these exceptional areas are found *recta, malverna,* and *granulata.* Otherwise the Coastal Plain appears to have acted as a rigid barrier for occupancy by *Allocapnia.*

The Mississippi Embayment, simply a north-central lobe of the Coastal Plain, shares this barrierlike characteristic except for a few peripheral records of *granulata* and *vivipara.* It is evident from the ranges of various *Allocapnia* species that there is no free traffic of clear-stream species across this area. A comparison of the ranges of *mohri* (Fig. 89) and *recta* (Fig. 90) demonstrates the point decisively.

THE ILLINOIS OZARKS CORRIDOR

The area called the Illinois Ozarks is a small unglaciated band of hills with a maximum elevation of about 1,000 feet extending across the southern end of Illinois. The area has numerous, clear spring-fed streams in rocky defiles and in these several *Allocapnia* abound. This hill country is separated by only the Mississippi River valley from similar hill country in Missouri and by only the Ohio River valley from hill country in Kentucky that is lower in elevation but nevertheless rich in artesian streams.

The northern flatland area extends to the base of the hills on the northern side of the Illinois Ozarks and the Mississippi Embayment extends slightly north of the Ohio River in Illinois to their southern flank. The Illinois Ozarks thus constitute a unique corridor of suitable *Allocapnia* habitats connecting the Cumberland Plateau-Appalachian area with the Ozark-Ouachita area of Missouri and southwestward. In the few small-stream *Allocapnia* species occurring in both areas, this circumstance has produced ranges shaped like an hourglass (*mystica,* Fig. 96; *rickeri,* Fig. 102).

THE NORTHEASTERN GATEWAY

Because of the east-west position of the flatlands, the northern end of the Cumberland Plateau and the Appalachians form a corridor of varied *Allocapnia* streams connecting extensive northern and southern areas inhabited by *Allocapnia.*

Allocapnia Dispersal Patterns

In attempting to adduce dispersal patterns in *Allocapnia,* one soon realizes that these patterns fall into two sharply defined categories. First are the instances in which a species occurs in a previously glaciated area; here it is obvious that the stonefly must have dispersed into the area since the last deglaciation. Second are the instances in which either the species does not now occur in a formerly glaciated area but for which there is evidence indicating a past range change, or that an ancestral form dispersed between two areas. In the first group both the approximate time and direction of dispersal are obvious — after the last major deglaciation and northward. In the second group neither time nor direction is immediately obvious.

In order to bring both categories into a cohesive general pattern, some means must be found to equate as well as is possible the circumstances of one category with those of the other. At this moment of writing the only equating factor is the amount of morphological difference between various contrasting species or sets of species. Such an equating is in reality one of the most dangerous attempts in phylogeny, that is, equating amount of change with duration of time. A high degree of probability is evident in Simpson's (1944) demonstration that rate of change normally varied modally within evolving lineages of a group, but that it might reach unexpectedly higher or lower values in a relatively small proportion of abnormally evolving lineages. On this basis, such correlations give as good an indication of the true course of events as is possible without additional data. Hypotheses advanced on such reasoning form a logical preliminary basis for summarizing present information.

By means of this time-change correlation, the *Allocapnia* dispersals outlined in the preceding section may be categorized into the following classes:

1. Ranges now found well into previously glaciated areas. Presumably post-Woodfordian (the last extensive glaciation of the Wisconsinan Ice Age). Examples include *minima* (Fig. 100), *nivicola* (Fig. 109), and *zola* (Fig. 103).

2. Extensive east-west ranges in which there is little or no variation between geographic extremes. Included are *vivipara* (Fig. 88), *mystica* (Fig. 96), and *rickeri* (Fig. 102). These ranges imply dispersals that probably occurred contemporaneously with those of Class 1.

3. Extensive north-south ranges along the axis of the eastern mountain chains in which there is little interpopulation variation. Included

are *virginiana* (Fig. 92), *loshada* (Fig. 89), and *aurora* (Fig. 105). These ranges also probably involved local dispersals that occurred simultaneously with those of 1 and 2.

4. Ranges having pronounced disjunctions in which the disjunct populations differ slightly. Included are *pygmaea* (Fig. 104) and *illinoensis* (Fig. 97). These disjunctions probably involved ancestral forms of the same age as the glacial maximum parents of Classes 1-3.

5. Ranges having disjunctions in which the disjunct populations differ sharply in one or more morphological characters. Included are *recta* (Figs. 90, 91) and *granulata* (Figs. 94, 95). The dispersing ancestral forms of these species presumably occurred before those of Classes 1-4.

6. Distinct sister species occurring in different regional areas, such that an ancestral widespread species must have become disjunct. Examples are the *frisoni-peltoides* pair, arising from Ancestor 25; the *unzickeri-warreni* pair, arising from Ancestor 24; and the *ozarkana-forbesi* pair, arising from Ancestor 26. The ancestors of these pairs of species must have dispersed prior to those of Class 5.

7. Ancestral forms occurring earlier in the family tree than those in Class 6, and necessarily representing widespread species that later became restricted and split into two or more offspring lineages. In this class are Ancestors 20, 15, and 27. On morphological grounds, the dispersals of these ancestors should have preceded those of Class 6.

8. Not included in the above categories except as implied phylogenetic informants are several species that have small ranges (*indianae*, Fig. 107; *ohioensis*, Fig. 106; and *curiosa*, Fig. 98), and 14 species that classify as local endemics (e.g., *brooksi*, Fig. 88; *polemistis*, Fig. 89). It is possible to fit these into some sort of dispersal scheme only as this is developed for better-known species of the genus.

Time Correlations

Only a decade ago it might have seemed logical to fit the preceding dispersal classes into a simple rational correlation with the then-understood pattern of late Pleistocene events (Rosholt et al., 1961). This was suggested by H. H. Ross (1965) for certain *Allocapnia* species. This earlier pattern presupposed an extensive Wisconsinan glaciation having a relatively uniform cold temperature at least as far south as central or southern Illinois. More recent geologic researches (Frye et al., 1968, 1969; Willman and Frye, 1969) have established that earlier concepts of midwestern Pleistocene events were an oversimplification of a much more complex glacial history.

In the Midwest and presumably also in eastern North America generally, Frye and his colleagues have unearthed evidence that the Wisconsinan had at least three successive warmer pulses alternating with three cold pulses, not including the shorter Valderan cold pulse of 11,000 years ago (Fig. 110). Previously this epoch had been considered as only a single cold pulse.

In the light of these new discoveries it is necessary to re-examine completely all previous ideas concerning *Allocapnia* Pleistocene dispersals.

EARLY HISTORY OF *ALLOCAPNIA*

The family Capniidae is primarily a boreal to subboreal group of stoneflies widely distributed across North America and Eurasia. From Fig. 4 it is seen that there have been many past dispersals of capniids between the two continents, including Ancestor 8, the parent of *Allocapnia* and its sister branch, the *vidua* group of *Capnia*. Going back further down the tree in Fig. 4, it is logical to conclude that Ancestor 5 was intercontinental and later its range was divided into two or more: the Eurasian and North American isolates. This probably occurred sometime in Pliocene or earlier when the temperate deciduous forest was fragmented in similar fashion. One North American isolate evolved into Ancestor 6, which subsequently gave rise to Ancestor 7 and the *manitoba-columbiana* lineage of *Capnia* and to Ancestor 8. Ancestor 7 was probably originally in western North America, Ancestor 8 in eastern North America.

Ancestor 8 in turn dispersed from North America to Eurasia. The high probability that Ancestor 7 was western, coupled with the rigid restriction of *Allocapnia* to eastern North American and the implication that its Ancestor 8 was also originally eastern, leads to the conclusion that Ancestor 8 dispersed from eastern North America to western Europe, following a course around the northern end of the Atlantic.

The ecological correlation of *Allocapnia* with the temperate deciduous forest supports the surmises concerning the possible Pliocene age of Ancestors 5, 6, and 8 of Fig. 4. *Allocapnia* would thus be a relatively young daughter genus arising from a branch of the older genus *Capnia*.

TRANSATLANTIC DISPERSALS

In recent years, most investigators have assumed that Cenozoic dispersals between Eurasia and North America occurred by way of the

Bering Bridge, from eastern Asia to western North America and vice versa. But gradually a surprisingly long list of instances has accumulated in which a transatlantic route appears more feasible. In addition to the *vidua* group cited above, several examples occur in the Trichoptera or caddisflies (Ross 1956). The *Rhyacophila stigmatica* group occurs only in Europe; its sister *Rhyacophila glaberrima* group occurs only in eastern North America. In the genus *Agapetus,* the *celatus* group occurs only in North America, the related *fuscipes* and *comatus* groups only in Europe. Additional examples occur in other groups of insects.

It now seems indicated that a considerable traffic of north temperate organisms occurred between eastern North America and Europe more or less contemporaneously with the spread of capniid Ancestor 8. These dispersals were probably at a period when the land areas of the North Atlantic were either still contiguous or closer together than at present (Dietz and Holden, 1970), and when temperate climates were more northerly than now.

THE APPALACHIAN-OZARK CORRIDOR

According to C. A. Ross (1963, 1965), during early or middle Pliocene when ancestral *Allocapnia* presumably evolved, the terrain between the Appalachians and the Ozarks was a relatively gently sloping surface and probably had few if any streams in which the genus could have survived. During the Pliocene (the epoch before the Pleistocene), considerable crustal uplift occurred, greatest along the Rocky Mountains and Appalachians and decreasing irregularly to the Mississippi Embayment and Gulf Coast areas. Local uplift occurred in the Ozark-Ouachita region and parts of the Cincinnati Arch. The elevation of the raised surfaces increased the gradient and promoted rapid erosion. The erosion produced many steep-sided valleys, breached the previous water table, and greatly increased the groundwater outflow in springs.

These events produced the series of special aquatic habitats suitable for *Allocapnia* that form an almost continuous corridor from the Appalachians to the Ozarks. The Illinois Ozarks are the narrowest part of this development.

Smaller areas southward in the Mississippi Embayment such as the Jackson Dome of Mississippi and the Monroe Uplift of southern Arkansas and northern Louisiana produced local areas having rocky, spring-fed streams, but these did not form a continuous southern corridor affording an *Allocapnia* dispersal route between the southern Appalachians and the Ouachitas.

It is almost certain that no *Allocapnia* species dispersed from the Appalachians to the Ozarks until the corridor of deep valleys and spring-fed streams had come into being. On this basis, Ancestor 3 of Fig. 86 might represent this first Appalachian-Ozarkian dispersal, and be considered late Pliocene in age. It is possible that the first Ozark colonist preceded Ancestor 3 and has become extinct, but of this we have no record.

LATER DISPERSALS

From the existence of Ancestor 3, with its possible dating of latest Pliocene or very early Pleistocene, there is a maximum of eight ancestral forms (including Ancestor 3) from Ancestor 3 to the immediate ancestor of any existing species. The evolution of all the known species of the genus therefore requires a minimum of only eight periods in which *Allocapnia* species expanded their ranges and underwent range division that resulted in isolated portions separated from each other long enough to become species.

The minimum number would be the actual number if ancestors at comparable levels of sequential speciation had indeed speciated at the same time. For example, if all speciations now represented by two species had come from ancestors that split up synchronously, then Ancestors 19, 22, 24, 25, 26, 30, and 34 would have existed and each split up at the same time. The amount of difference between the species in each pair is roughly comparable, lending support to the probability of ancestral synchrony. Similar circumstances are found at the next possible level of ancestral synchrony, involving Ancestors 2, 21, 23, 27, 29, and 33.

In addition to a rough measure of morphological similarity, ecological comparisons add support to the idea of ancestral synchrony. Thirty-four of the 38 species of *Allocapnia* have the same general ecological requirements — a small, clear, rocky stream. The exceptional four species are scattered through the family tree (*vivipara*, *granulata*, *minima*, and *pygmaea* in Fig. 86), indicating that each species evolved its different ecological characteristics independently from an ancestor having ecological requirements similar to most of the 34. From this conclusion there is a good likelihood that all the numbered ancestors in Fig. 86 had nearly the same ecological tolerances, and could be expected to have reacted synchronously to changing environmental conditions.

If we admit this evidence as substantial support for considerable synchrony of speciation in various lineages, we must still account for nine successive periods, each conducive to speciation. Each period would need to provide (for *Allocapnia*):

1. A cooler and presumably wetter period that would displace populations or allow them to disperse to new areas, and
2. A warmer and drier period that would cause breaks in the expanded ranges, the breaks continuing sufficiently long that the newly isolated populations evolved into distinct species.

Functionally these circumstances are illustrated by several species. The populations of *recta* involving ancestral and derived forms in Alabama illustrate a circumstance in which the first step occurred but the duration of the isolation step was too short to allow time for the evolution of genetic and sexual isolation. As a result, the *recta* populations of southern Alabama are a hybrid flock of the two morphological types (Figs. 90, 91). Widespread *granulata* is a similar, but more complex, example of the same phenomenon (Figs. 94, 95). The two sister species *ohioensis* and *indianae* (Figs. 106, 107) illustrate an instance in which the second step was sufficiently long that the once-isolated populations became distinct species (Ross and Freytag, 1967).

Glacial Stages and Speciation. There are three obvious possibilities to account for the nine or more speciation pulses needed to explain the phylogeny of *Allocapnia* since late Pliocene time: intraglacial speciation (occurring within a particular glacial stage), interglacial speciation (requiring a full glacial stage and its succeeding warm interglacial stage), or some combination of the two.

Intraglacial speciation. Regarding *Allocapnia*, we have detailed morphological and geographic data that appear to indicate a correlation with certain intra-Wisconsinan events, but none that have any firm correlation with earlier intraglacial events. The discussion of intraglacial speciation is based therefore only on the Wisconsinan.

A set of conditions that might account for *Allocapnia* speciation is the alternation of climatic pulses occurring *within* each glacial stage. Four of these are well documented for the Wisconsinan in both North America and Europe (Butzer, 1964; Frye et al., 1969), not counting Recent (Fig. 110). Each pulse is associated with a glacial advance of 8,000-10,000 years and a nonglaciated period of about the same length. Computed ocean paleotemperatures indicate that temperatures during the unglaciated periods were lower than those of today. Studies in Wisconsin by Black (1964, 1965) suggest that the climate there during the Farmdalian interglacial substage was considerably cooler than today.

If these calculations are correct, then we can make a reasonable reconstruction of the behavior of certain *Allocapnia* species during the Wisconsinan. The climates of the last 6,000 years are good examples of possibly the warmest interglacial periods within the Wisconsinan. If another glacier were to descend, with accompanying colder weather, the more northern extensions of widespread species that now extend into previously glaciated areas would disintegrate but populations to the south would probably be little affected. During the next warmer spell the same species would repopulate the deglaciated northern areas. There are virtually no present-day ranges that such an oscillation would break into new isolated segments for a long period of time.

It is likely that such past intrastage oscillations produced the hybrid flock of ancestral and derived *recta* in southern Alabama (Fig. 91). If so, presumably only two of the four warm-cool pulses of the Wisconsinan affected these populations. Perhaps this apparently restricted oscillation of *recta* indicates that the differential climatic effect of intrastage pulses was almost completely suppressed at that distance from the glacial fronts.

If the peregrinations of *granulata* occurred within the Wisconsinan, they would seem to be correlated with all four of the warm-cool pulses. The case of *granulata* is puzzling, because its western populations evolved modest morphological differences, whereas in equally widespread species such as *mystica* and *rickeri* no such phenomenon occurs. As suggested earlier, this discrepancy is easily explained if *mystica* and *rickeri* occupied a relatively compact or small contiguous range throughout most of the Wisconsinan, then dispersed relatively rapidly in either later Wisconsinan or post-Wisconsinan.

The intraspecific variation in *recta* and *granulata* supports the idea that, in *Allocapnia,* distinctive species did not evolve during the Wisconsinan but required longer periods of geographic isolation.

Interglacial speciation. The conventional Pleistocene calendar (Fig. 111) accounts for only 3½ long-term pulses (not including glacial oscillations within the Wisconsinan). If the Pleistocene had followed earlier glacial oscillations beginning in the Pliocene, we might attribute the needed 5½ temperature pulses to pre-Pleistocene perturbations in the Pliocene. Beard (1969) presents evidence from deep-sea cores in the Gulf of Mexico that the Pleistocene began abruptly about 2.8 million K-Ar years ago, thus indicating that some other explanation is necessary to account for the early climatic pulses needed to explain the *Allocapnia* speciation pattern.

Combined intraglacial-interglacial speciation. A possible answer involves a point stressed by Frye et al. (1969) concerning Pleistocene investigations in general. They point out that as new study techniques have become available, at least with reference to terrestrial data, we have been able to detect greater detail of glacial and temperature oscillations in the geological record. It may very well be that the Illinoian, Kansan, and Nebraskan glacial stages (4, 3, and 5 times as long as the Wisconsinan, respectively) may each have consisted of two or more long-term pulses of cold and warm climates, pulses not detectable by present analytic techniques.

It is possible that most if not all the nine cold-warm pulses required to explain the *Allocapnia* speciation pattern did occur during the calculated 2.8 million years comprising the Pleistocene (Beard, 1969). This surmise does not rule out the possibility that some of the earlier *Allocapnia* speciations may have occurred during wet-dry cycles or as yet undetected cold-warm cycles of the 12 million years comprising the Pliocene.

If most of the *Allocapnia* speciation pattern occurred during the Pleistocene, then many of the upper-level ancestors of Fig. 86, including Ancestors 19, 22, 24, 25, 26, 30, and 34, dispersed during the Illinoian glacial stage (Fig. 111). Their ranges were broken and the parts isolated during the Sangamonian interglacial stage. The resultant two species arising from each of Ancestors 22, 30, and 34 dispersed and became sympatric during the Wisconsinan glacial stage (Figs. 108, 109). Carrying this account into the future, certainly the range of *nivicola* will be fragmented if the future climate of eastern North America is a hot one like that of the Sangamonian interglacial.

POST-WOODFORDIAN DISPERSALS

Up to this point we have made no mention of the possible effect on *Allocapnia* evolution of the climatic cycles that occurred after the last major and extensive ice advance, the Woodfordian substage (Fig. 110). Smith (1957) and others have demonstrated the use of postulated post-Woodfordian climates for interpreting the dispersal of vertebrates into previously glaciated terrain. The question arises as to whether these same events, encompassing the last 12,000 years, can shed light on either dispersals or other evolutionary developments of *Allocapnia*.

There is a good possibility that the isolated population of *nivicola* in Wisconsin (Fig. 109) resulted from a dispersal via spring-fed streams from central Indiana, around the base of the Great Lakes, and northward into Wisconsin. Springs now devoid of *Allocapnia* and others on record but now destroyed could have been strategic steppingstones along such a route. The dispersal of *rickeri* into its present northwestern outposts (Fig. 102) was undoubtedly post-Woodfordian, and may have occurred during a recent pluvial period in a stream-by-stream progression up the Mississippi Valley before man tampered seriously with the environment.

In light of the marked morphological differences between different populations of *recta* and *granulata,* here thought to have evolved during the Wisconsinan, it is odd that the isolated Missouri population of *pygmaea* is so similar to the others. The disjunction producing this isolation was at first considered to date from early Wisconsinan (Ross et al., 1967). Now there is need to consider the possibility that *pygmaea* dispersed from the East into its present northern range (Fig. 104) during the Farmdalian or Two-creekan substages and moved from Minnesota and Wisconsin into Missouri during the ensuing glacial substage.

Concerning *granulata,* the last meeting of the eastern and western strains in eastern Missouri and western Illinois and possibly in Louisiana was undoubtedly during a pluvial part of post-Woodfordian time. The small amount of hybridization now in evidence indicates that the contact was either of short duration or involved only small numbers of individuals.

EVOLUTION OF LOCAL ENDEMICS

One circumstance indicating considerable pre-Wisconsinan evolution of *Allocapnia* concerns endemic species. Of the 38 species known, 14 classify as local endemics occurring considerably south of the maximum glacial fronts:

brooksi and *tennessa* (Fig. 88)
polemistis (Fig. 89)
fumosa, unzickeri, warreni, and *peltoides* (Fig. 93)
zekia (Fig. 96)
ozarkana (Fig. 98)
jeanae (Fig. 101)
cunninghami, perplexa, sandersoni, and *stannardi* (Fig. 103)

In addition, *mohri* and *loshada* (Fig. 89) have relatively small ranges also well south of the maximum glacial fronts. None of these 16 species gives any indication of range movements in the immediate past. All but three seem to be restricted rigidly to artesian streams. The three exceptions are *brooksi, fumosa,* and *stannardi,* restricted, or nearly so, to cascades in the Great Smoky Mountains, an unusual habitat from the standpoint of *Allocapnia.*

It appears that all 16 species have become so narrowly adapted to the locations where they occur as to be unable to disperse from them. This means that they are unable to survive in streams fed chiefly by surface run-off in those areas. It has been suggested that chemical composition of the water is the cause of this ecological restriction. It seems more reasonable to suppose that the cause of restriction is uniformity of temperature throughout the entire year. Underground water usually issues at the mean annual temperature for the region, varies extremely little from winter to summer, and if the stream is undiluted the temperature effect carries a considerable distance downstream. The deeper, narrower, and more heavily wooded is the valley, the greater is the distance of uniform temperature in the stream.

Ecological specialization to the degree exhibited by these local endemics seems to be explainable only by a lack of genetic plasticity concerning temperatures other than those in the occupied habitat. Interspecific competition might be invoked, but seems not to apply because the more widespread species occur abundantly in the same streams as do the local endemics.

The simplest way to explain the situation is to suppose that each endemic originated from a widespread parent such as the present-day *mystica* or *rickeri* (Figs. 96, 102) that spread to areas of artesian streams during a climatic period such as the present. Subsequently the climate became much warmer and/or drier, causing nonartesian streams to become markedly warmer in summer or to dry up in seasons of decreased rainfall. The range of the parent species would then be broken into isolated fragments, some situated in an artesian area. In each artesian area, any individuals dispersing out of the area would not reproduce. As a result, the population in each isolated segment would build up a genetic constitution adapting it only to the isolated area occupied by the population. The adaptive tolerance of the population would tend toward a much narrower spectrum than that possessed by the widespread ancestral form that was the original parent of the isolated population. In time, through negative selection, the entire colony would end up with an ecological tolerance only great enough to succeed in the world of restricted artesian temperatures. The longer the period of hot climates, the more dependent would be the isolated population on the artesian habitat. If the dependence were sufficiently great, when the climate became cooler or wetter, the seasonal temperature fluctuations inherent throughout the *Allocapnia* range would be a barrier to the dispersal of the artesian-adapted species.

The model best suited for such a series of adaptive changes in *Allocapnia* would be a correlation with the hot interglacial stages (Fig. 111). Each of these would have provided warm surface streams in which *Allocapnia* could not survive, and would have lasted long enough to exert the above-postulated selection pressures for a period of at least 50,000 years.

In this model, temperature and not decreased rainfall would have been the critical factor. The model requires an abundance of artesian water throughout the period, and this water originally comes from rainfall in or within a few hundred miles of the occupied area. Presumably the rainfall was adequate to provide the necessary artesian flow.

If these local endemics had dispersed and evolved during the substages of the Wisconsinan (Fig. 110), there would need to have been temperature conditions during these mid-Wisconsinan substages as high as or higher than those occurring now. Evidence so far at hand indicates the opposite (Black, 1964, 1965). Also, if these endemics had been of intra-Wisconsin origin we should expect to find more isolated outposts of some of the species, as for *illinoensis* (Fig. 97), or a larger number of closely related sister species.

To make the model operable on a continuing basis, one more postulate must be made. The local isolation and selection pressures described would seem to drive the evolution of the genus in the direction of an assemblage of local endemic species having no power to disperse again. Yet the genus now contains 17 species that have been able to disperse into previously glaciated regions, 10 of them extensively. Two circumstances appear to be involved. First, some lineages appear to have maintained linear ranges extending north of the Appalachians and southward through them. Each of these species would presumably live in many varied habitats, considering the ranges as a whole, and would therefore be under selection pressures favoring a wide ecological tolerance. During a cold glacial period these genetically labile species would be those dispersing widely in the area south of the glaciers, as in *rickeri* (Fig. 102) and *pygmaea* (Fig. 104), and their southern outpost populations would be stranded by the next interglacial period with the possibility of forming new local endemic species.

Second, some restricted species may in some fashion have gained or regained a wider ecological tolerance. Such events are suggested by *rickeri, vivipara,* and *mystica.* Each has a wide present range (Figs. 88, 96, 102) but no trace of geographic variation. Their relatives have small ranges. Altogether, these circumstances suggest that each evolved as a small population and became able to disperse widely while their relatives did not.

SUMMARY

The stonefly genus *Allocapnia* occurs only in eastern North America. It is associated with the temperate deciduous forest except for the species *minima* that reaches the northern tree line. All species emerge as adults during the winter or early spring. The genus represents a branch of the large and worldwide genus *Capnia*. Thirty-eight species of *Allocapnia* are known, of which a few pairs hybridize. On the basis chiefly of male and female genital characters, a highly probable family tree of *Allocapnia* has been constructed.

When geographic distribution was integrated with this phylogeny, dispersal paths for present species and hypothetical ancestral species were adduced. The genus apparently evolved primarily in association with the Appalachian Mountain system, its neighboring ridges, and areas northeast of them. Six ancestral lineages spread to the Ozark-Ouachita Mountain region, but not synchronously, and the resultant western isolated populations evolved into distinct lineages, one of which spread to the Appalachians and reversed the process.

A summation of geologic and paleoecologic evidence indicates that *Allocapnia* probably arose in the Pliocene from an eastern ancestor that also spread by a circumatlantic route to western Europe, the segregate there evolving into the *vidua* group of *Capnia*. The continuing eastern North American form evolved into *Allocapnia*. The evidence at hand suggests that all the phylogenetic developments of the genus that we can deduce started late in the Pliocene when tectonic uplifts in central North America and subsequent intensified erosion had produced an avenue of spring-fed streams that allowed dispersal of the genus between the Appalachian and Ozark-Ouachita systems. The evidence further suggests that the speciation pattern of *Allocapnia* is associated with the alternation of cold glacial and warm interglacial periods of the Pleistocene and comparable climatic oscillations occurring in late Pliocene. According to this suggested model of speciation, the genus as we know it is three or four million years old.

ACKNOWLEDGMENTS

In our studies of *Allocapnia* and the preparation of this report we have received a great deal of help from many persons. Without the wholehearted cooperation of the collectors we fondly call the Winter Stonefly Club we could not have begun to assemble the vast collection on which the study is based. The club membership is as follows:

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W. D. Youngs, New York Conservation Department, Ray Brook, N.Y.

Valuable study efforts and curatorial assistance were provided by T. Yamamoto, G. Rotramel, T. L. Harris, and R. T. Allen. Expert clerical assistance was afforded by Mrs. Bess White, Mrs. Bernice P. Sweeney, and Mrs. Dorothy Gailus.

Figures 1-3 were done by Dr. C. O. Mohr, the illustrations of the male genitalia by Mrs. Alice Prickett, those of the female genitalia by Mrs. Diana Slavens, and the maps were executed by Mr. Richard Sheets. Mrs. Prickett was invaluable in assembling the plates.

Although they are not responsible for the conclusions we reached, we received valuable geological advice from Drs. J. C. Frye, H. B. Willman, and J. Kempton of the Illinois Geological Survey and Dr.

C. A. Ross of Western Washington State College. Welcome advice and encouragement were received from Drs. H. B. Mills, P. W. Smith, and George Sprugel, Jr., of the Illinois Natural History Survey.

Financial support for a considerable part of the project was afforded by the National Science Foundation.

To all these and to others whose names we may have omitted inadvertently we extend our sincere thanks.

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FIGURES

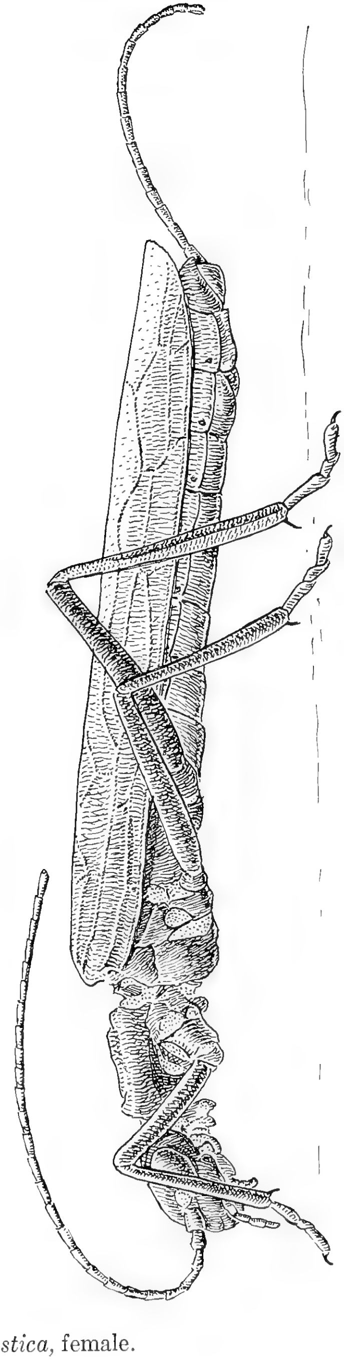


FIG. 1. *Allocapnia mystica,* female.

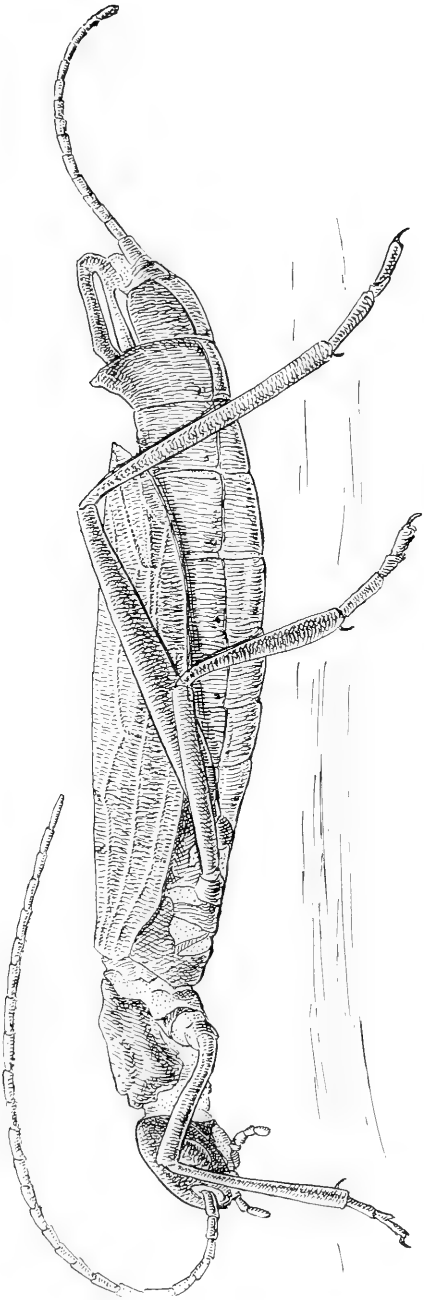


Fig. 2. *Allocapnia mystica*, male.

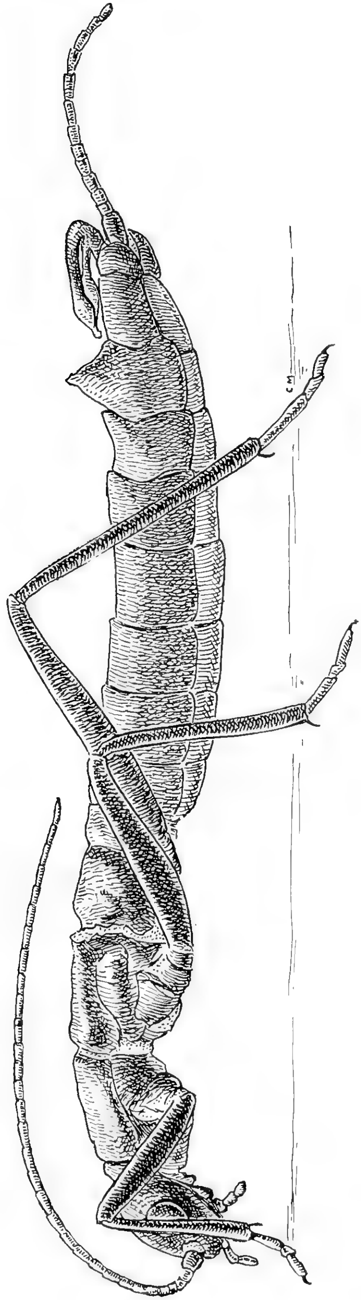


Fig. 3. *Allocapnia vivipara,* male.

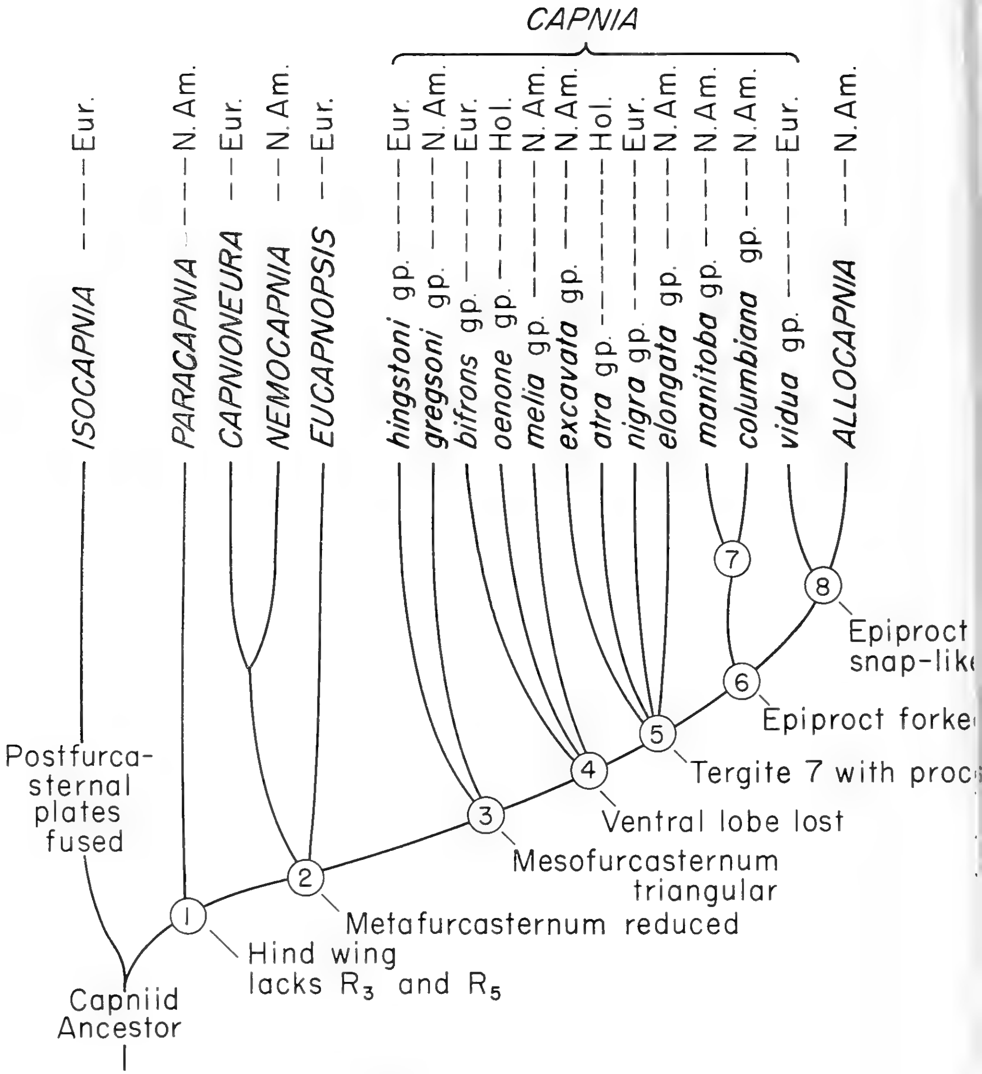
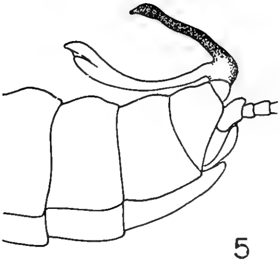


Fig. 4. Preliminary phylogenetic outline of the family Capniidae. *Eur.*, Eurasian; *Hol.*, Holarctic; *N. Am.*, North American.



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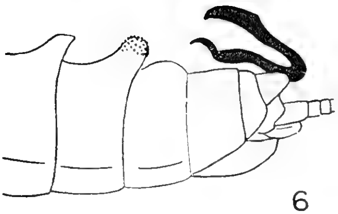

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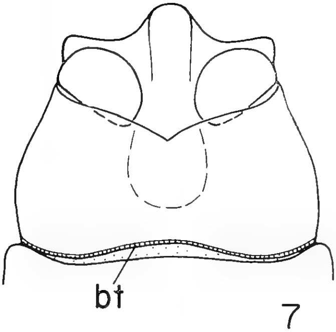

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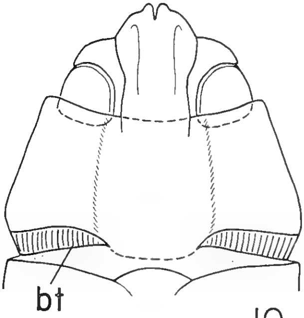

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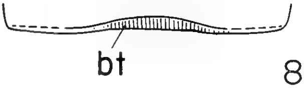

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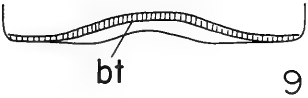

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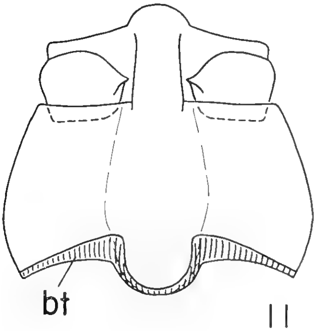


11

Fig. 5. Terminal segments of male *Capnia columbiana* Claassen, illustrating V-shaped epiproct. (After Nebeker and Gaufin.)

Fig. 6. Terminal segments of male *Capnia vidua* Klapalek, illustrating the double-limbed epiproct of the appressed type. (After Aubert.)

Fig. 7. Dorsal aspect of ninth segment of male *Capnia glabra* Claassen. *bt*, basal thickening (in Figs. 8-11 also).

Fig. 8. Basal thickening of ninth tergite of male *Capnia manitoba* Claassen.

Fig. 9. Basal thickening of ninth tergite of male *Capnia columbiana*.

Fig. 10. Dorsal aspect of male ninth segment of *Capnia vidua*.

Fig. 11. Dorsal aspect of male ninth segment of *Allocapnia loshada*.

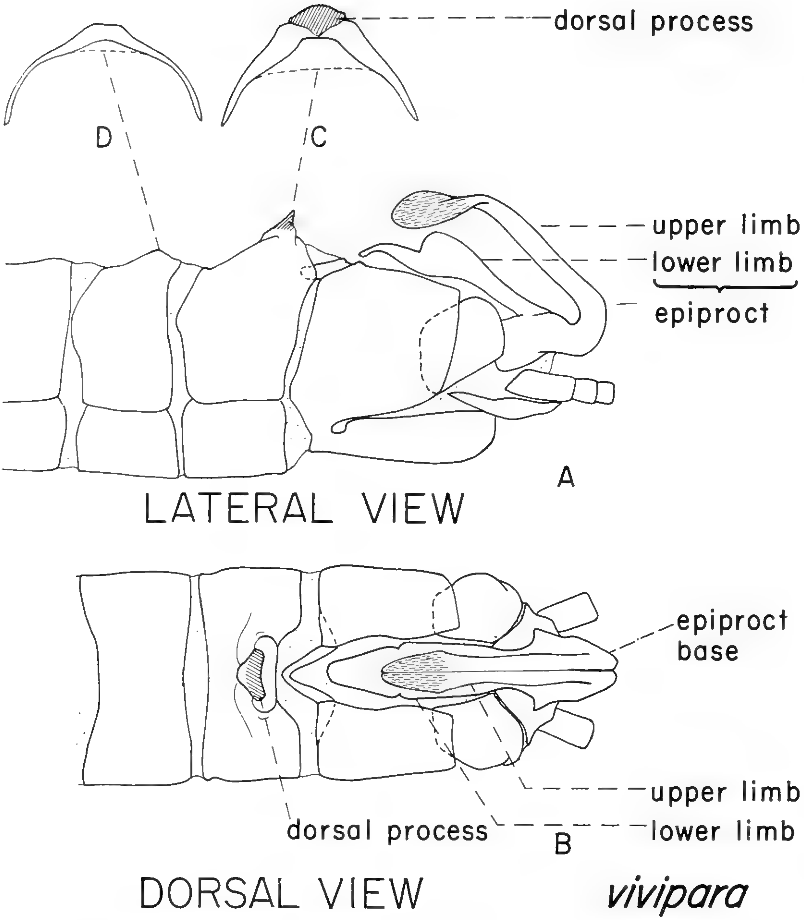
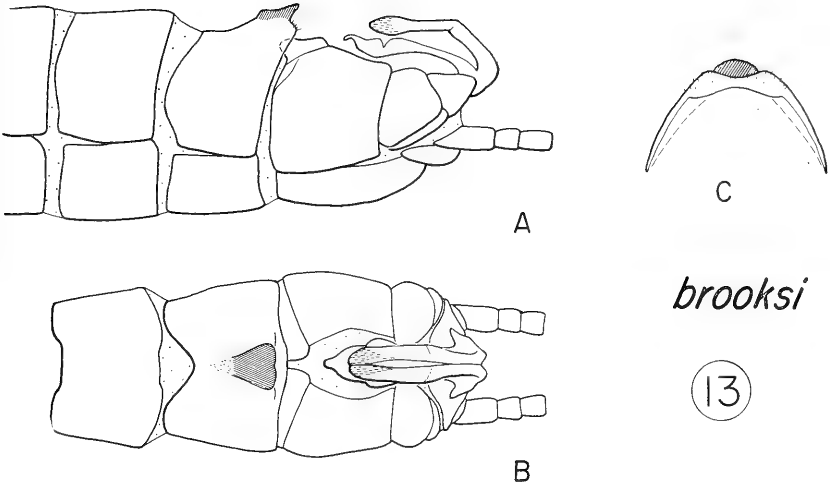
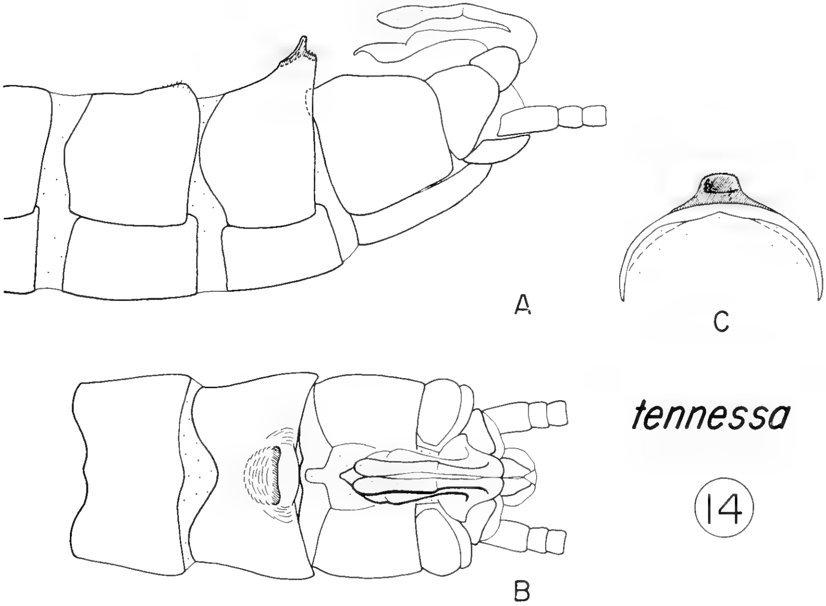
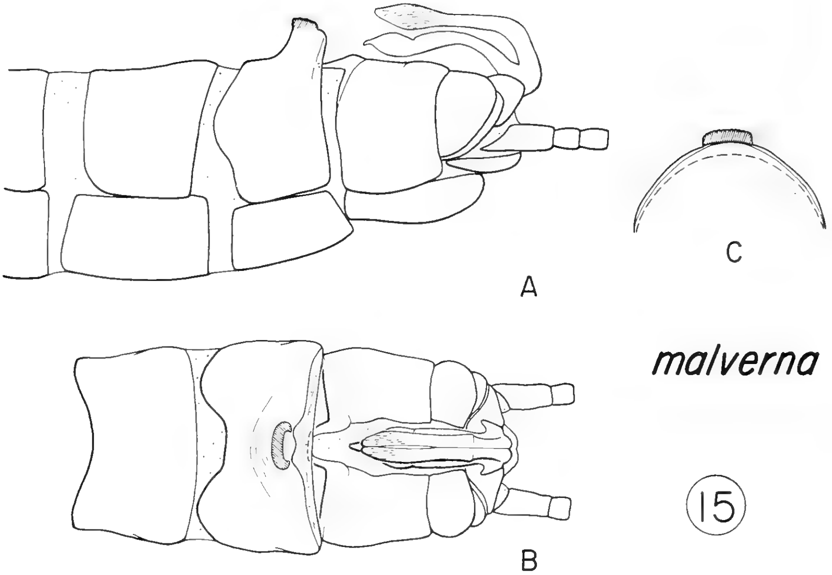


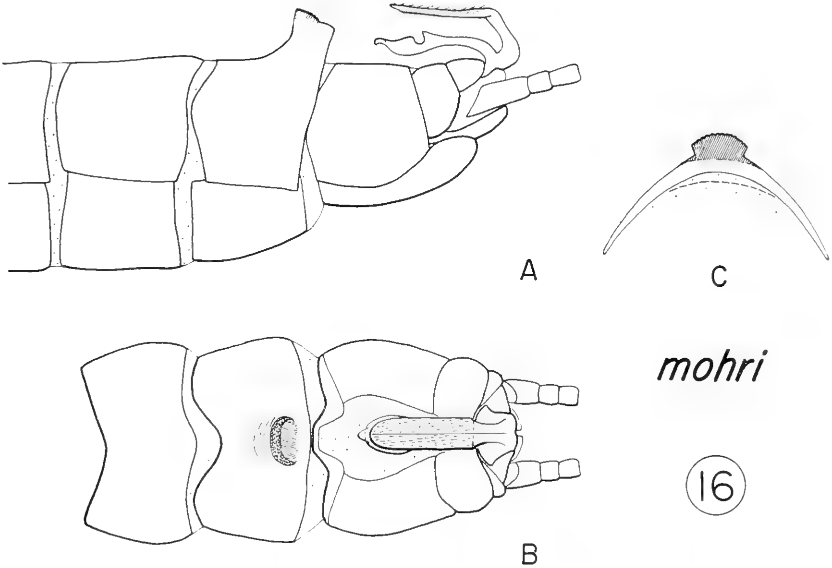
FIG. 12. Terminal abdominal segments of male *Allocapnia vivipara*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.



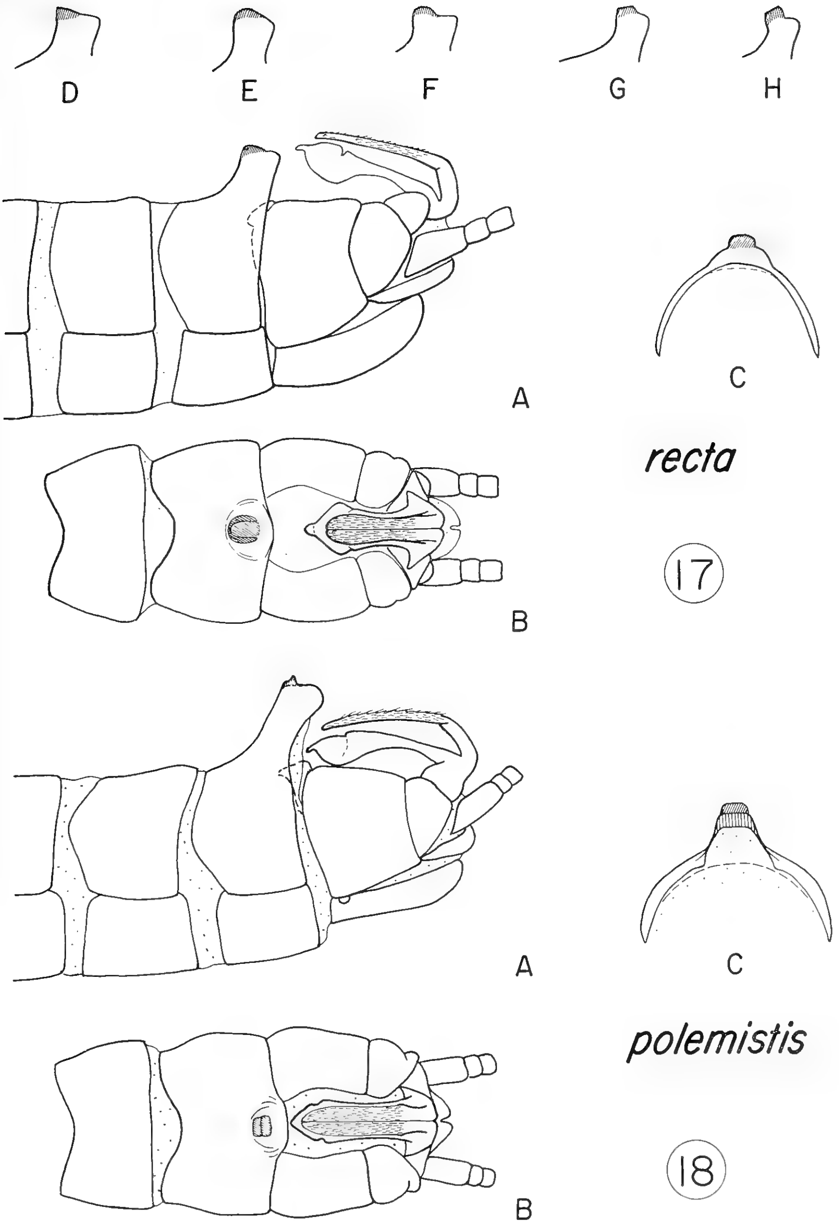


Figs. 13, 14. Terminal abdominal segments of male *Allocapnia brooksi* and *tennessa*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.

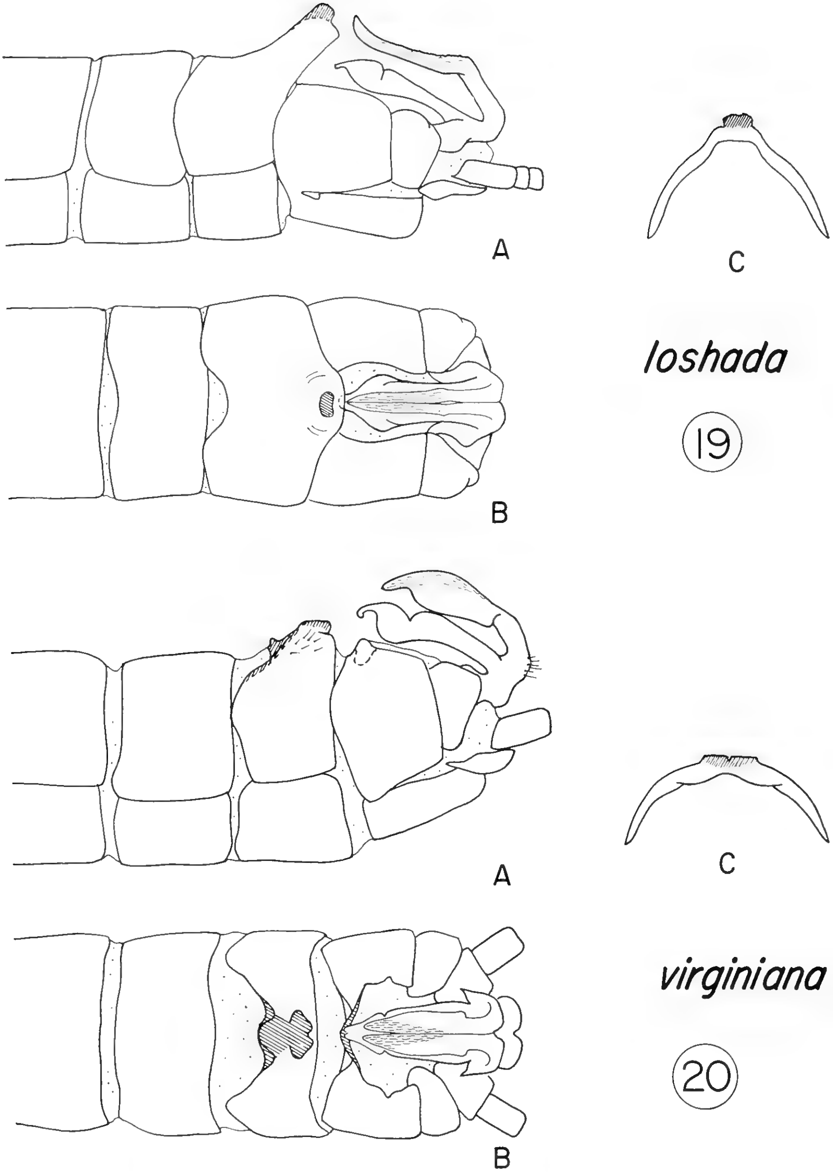




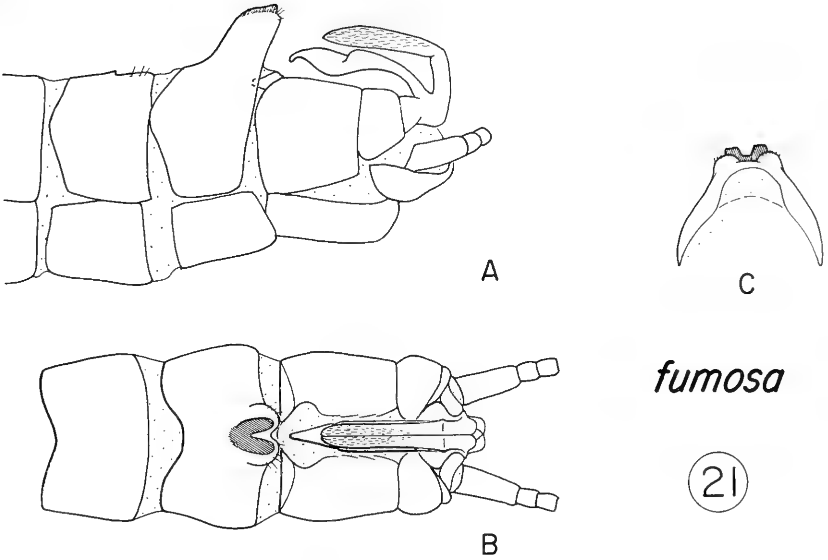
Figs. 15, 16. Terminal abdominal segments of male *Allocapnia malverna* and *mohri*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.

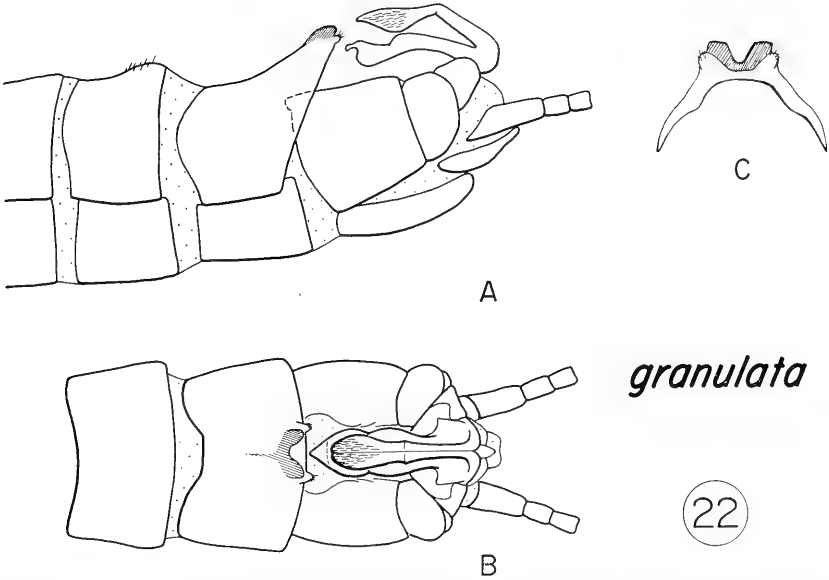


FIGS. 17, 18. Terminal abdominal segments of male *Allocapnia recta* and *polemistis*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D-H*, variants of dorsal process of eighth tergite, lateral aspect. *D*, ancestral type; *G, H*, derived type; *E, F*, intermediate types.

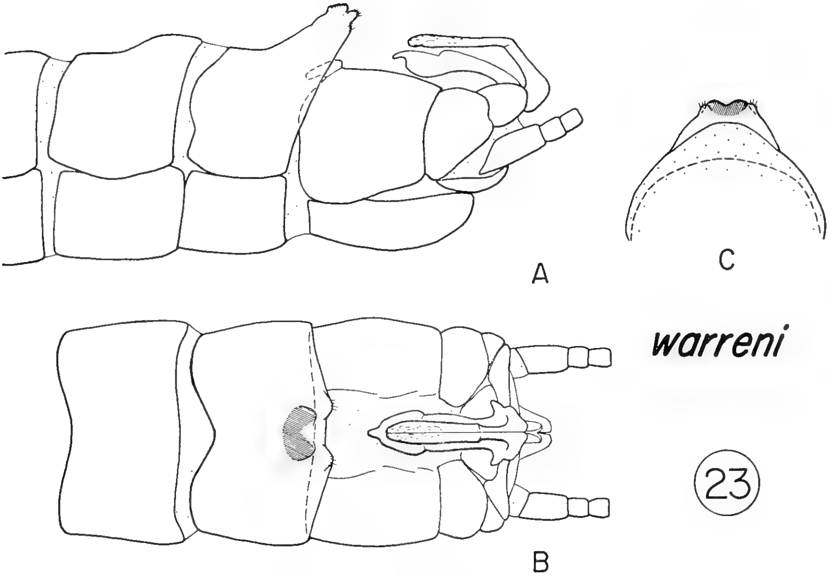


FIGS. 19, 20. Terminal abdominal segments of male *Allocapnia loshada* and *virginiana*. *A*, lateral aspect; *B*. dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.





FIGS. 21, 22. Terminal abdominal segments of male *Allocapnia fumosa* and *granulata*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.



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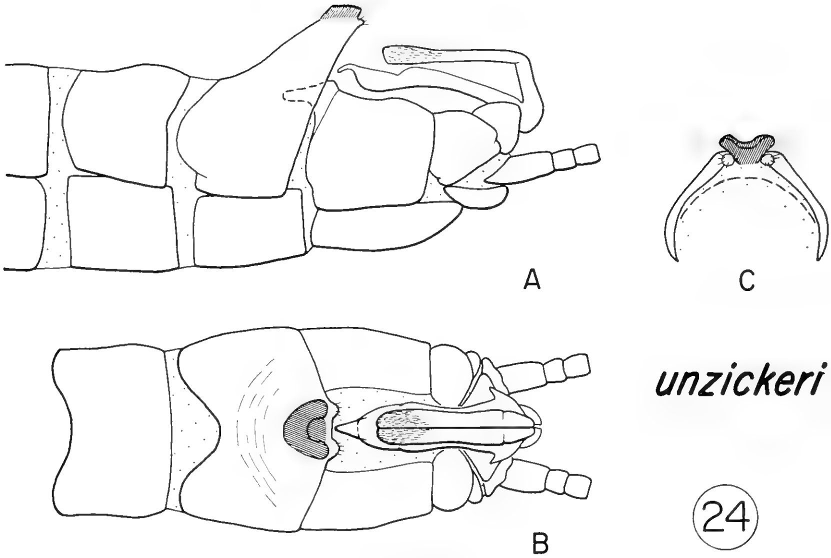

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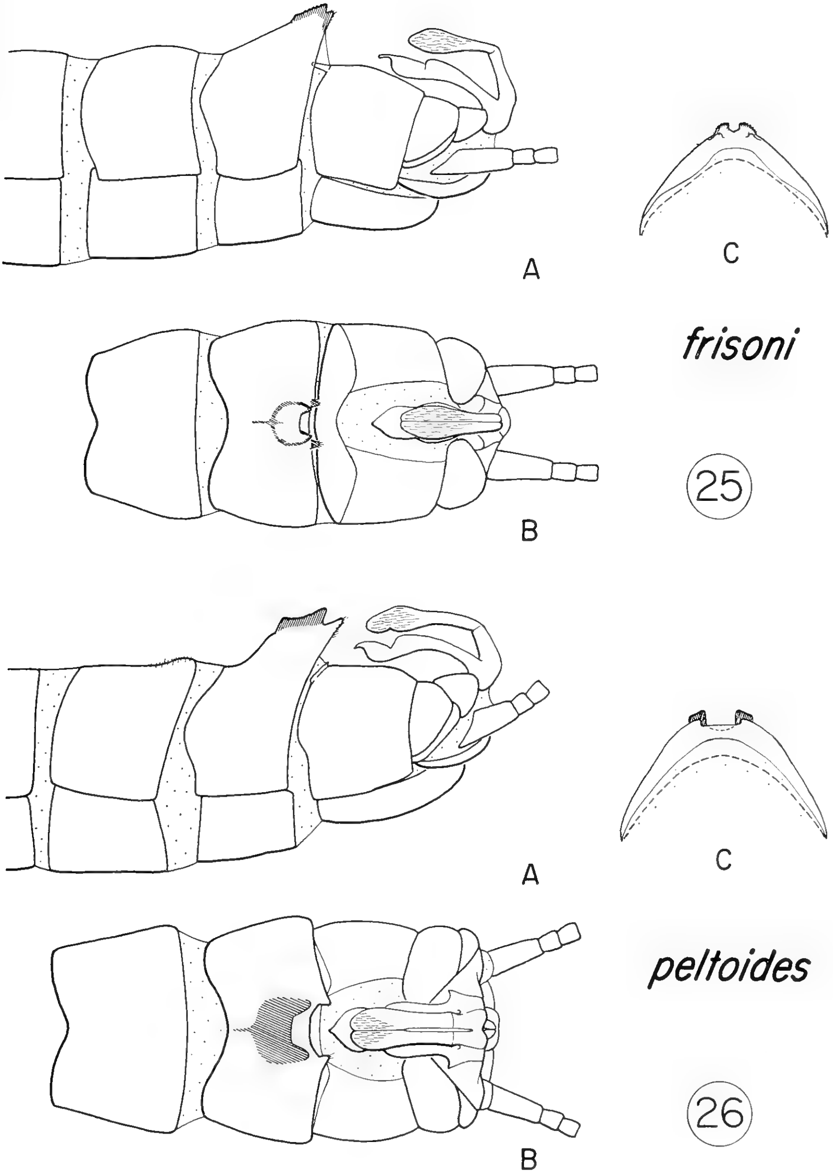
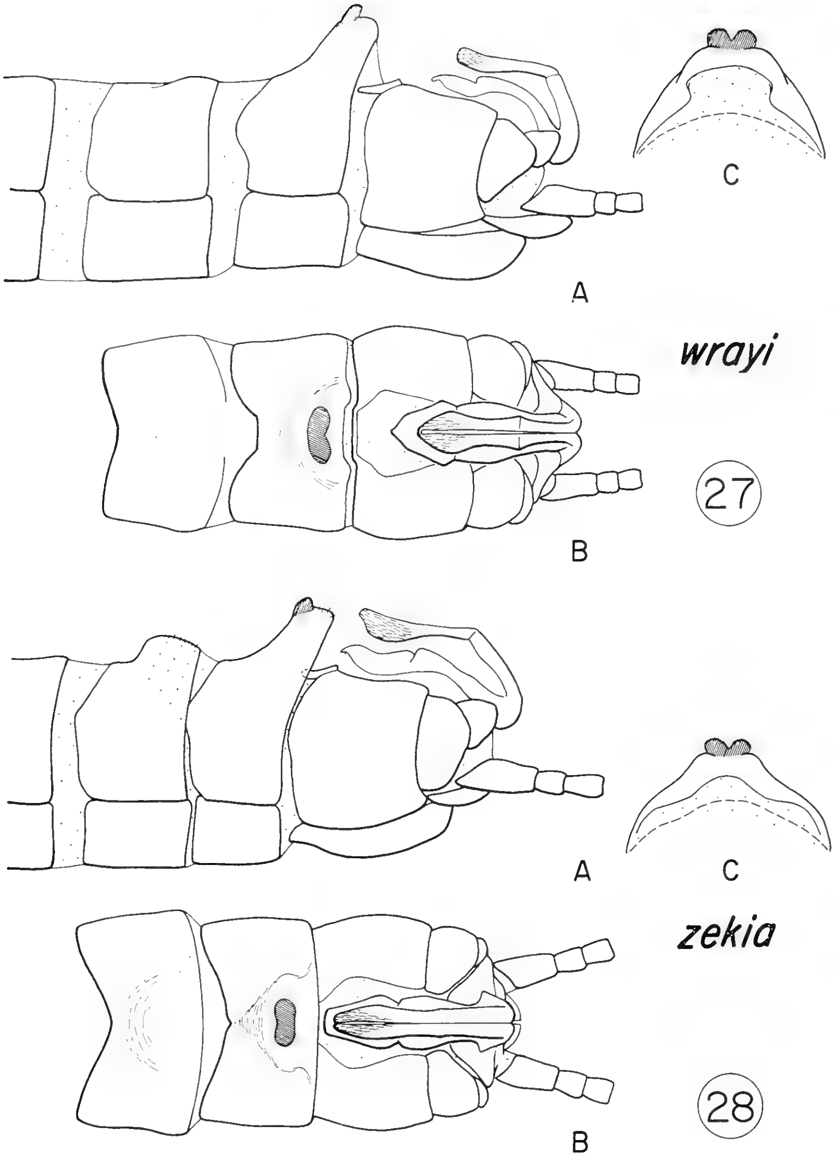
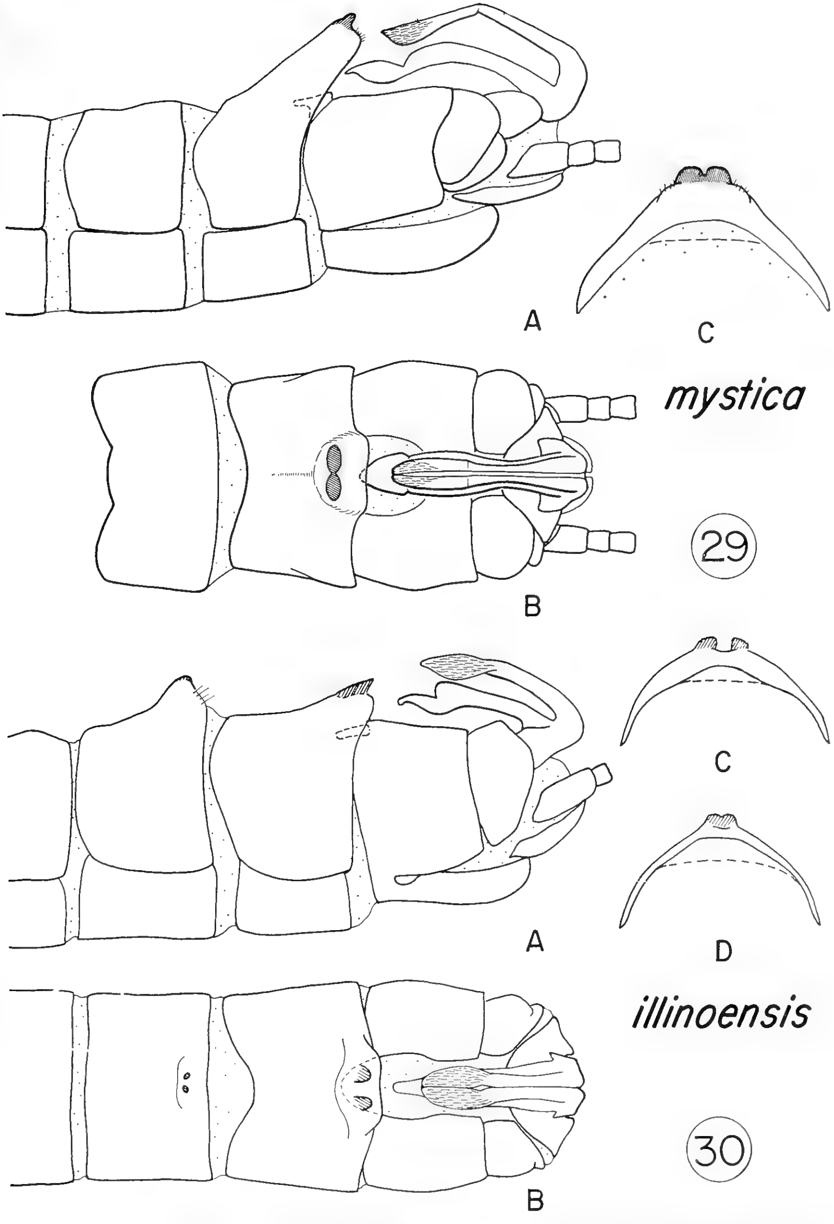
FIGS. 23, 24. Terminal abdominal segments of male *Allocapnia warreni* and *unzickeri*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.



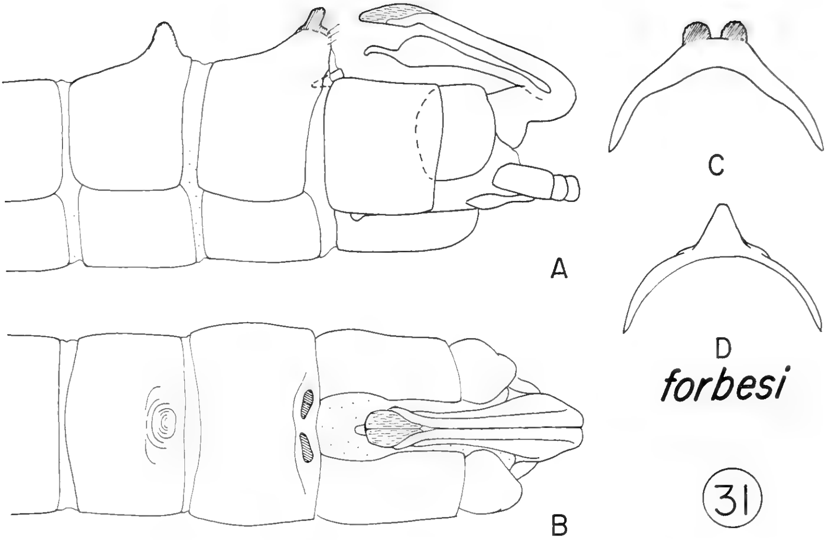
Figs. 25, 26. Terminal abdominal segments of male *Allocapnia frisoni* and *peltoides*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.

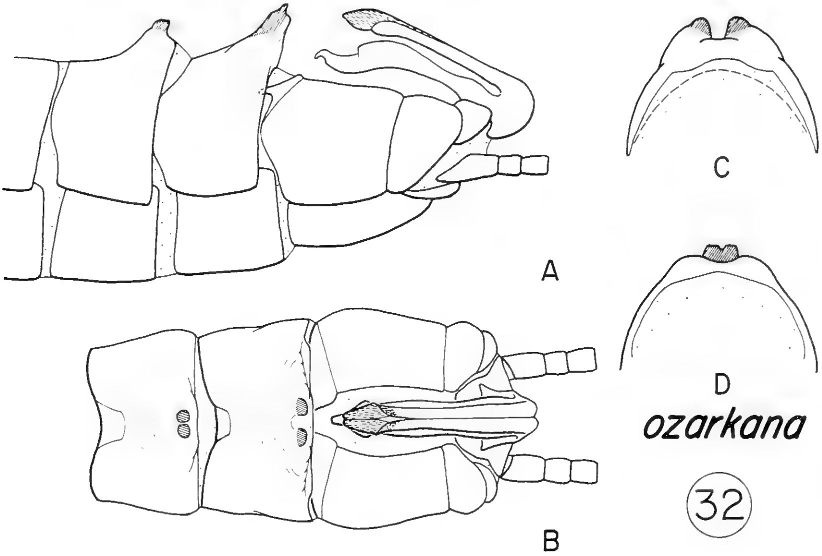


Figs. 27, 28. Terminal abdominal segments of male *Allocapnia wrayi* and *zekia*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite.



Figs. 29, 30. Terminal abdominal segments of male *Allocapnia mystica* and *illinoensis*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.





FIGS. 31, 32. Terminal abdominal segments of male *Allocapnia forbesi* and *ozarkana*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.

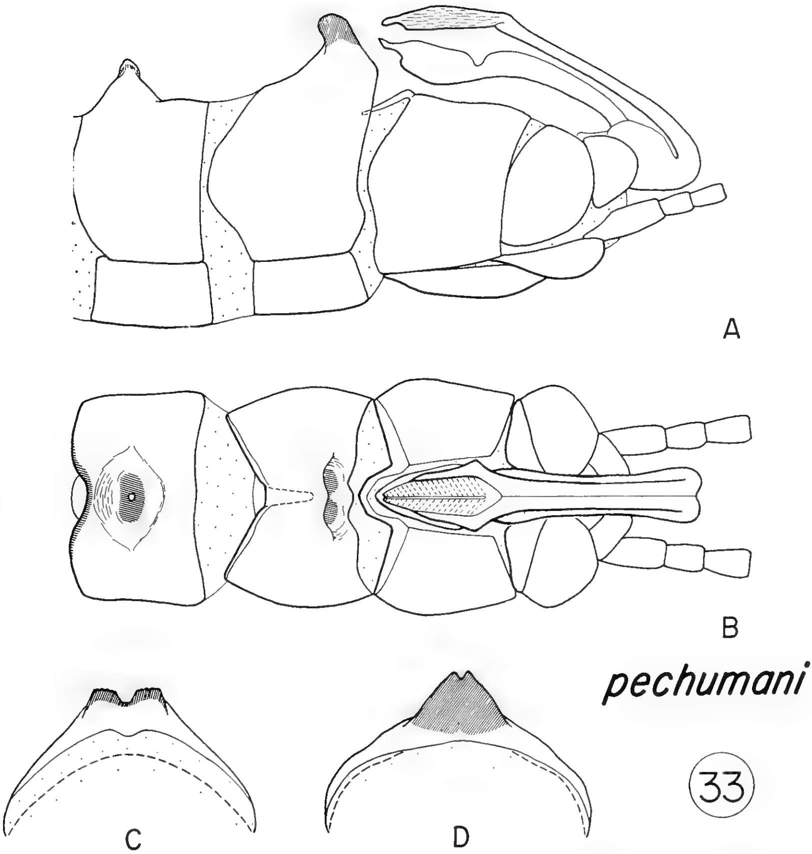
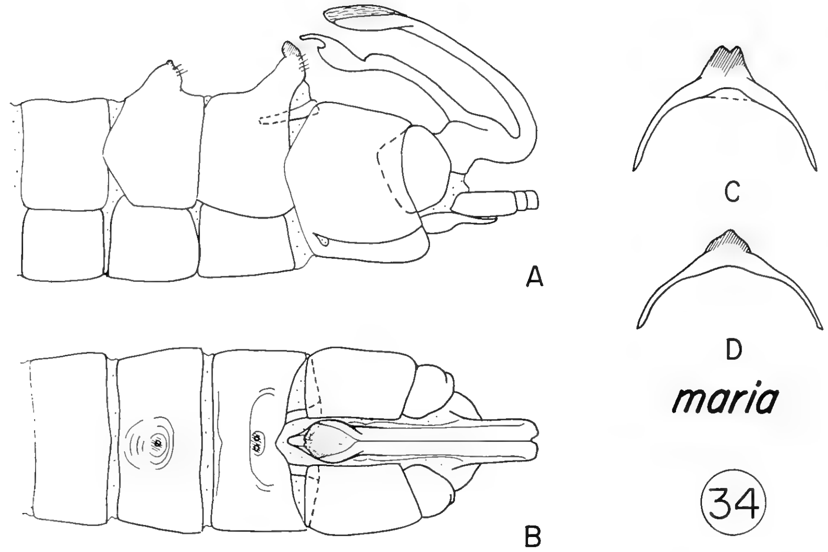
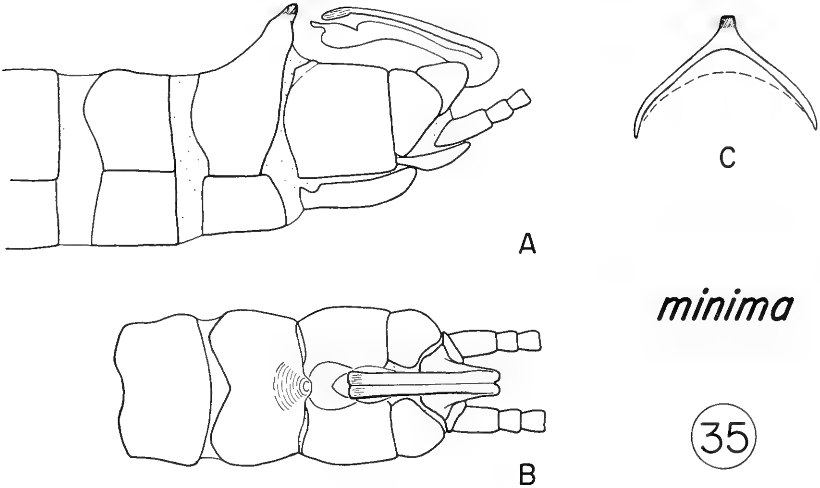
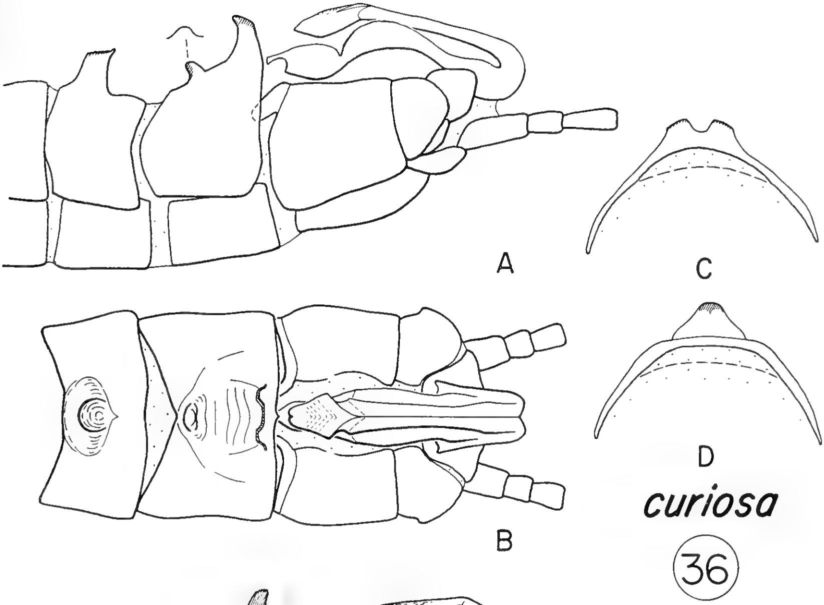


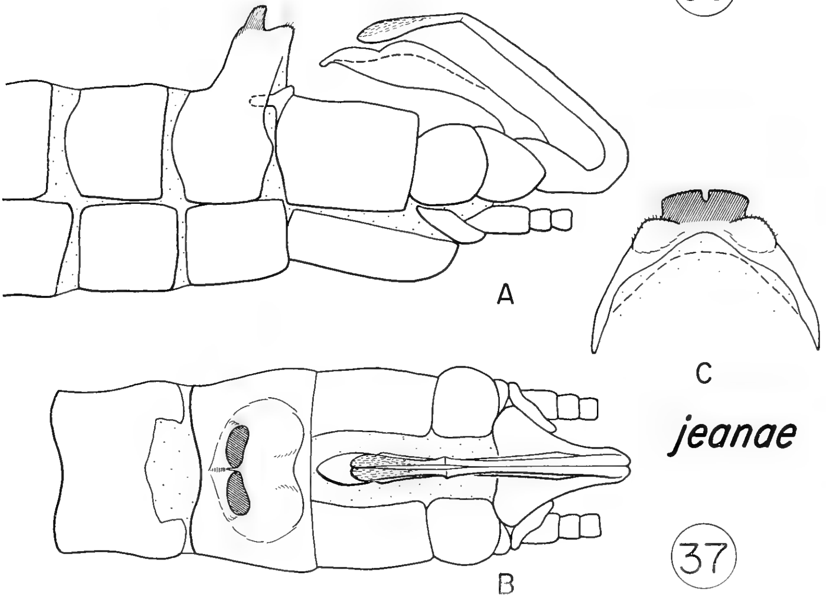
FIG. 33. Terminal abdominal segments of male *Allocapnia pechumani*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.



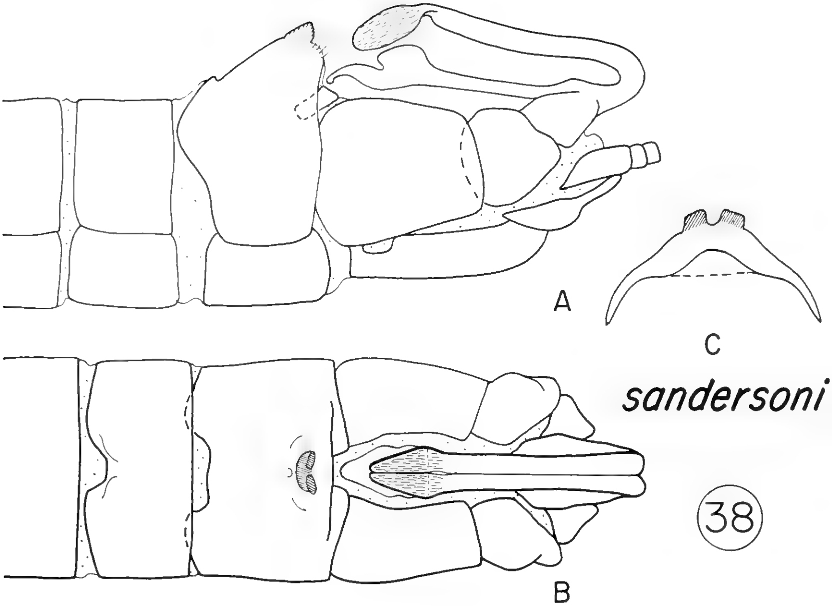


Figs. 34, 35. Terminal abdominal segments of male *Allocapnia maria* and *minima*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.





Figs. 36, 37. Terminal abdominal segments of male *Allocapnia curiosa* and *jeanae*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.



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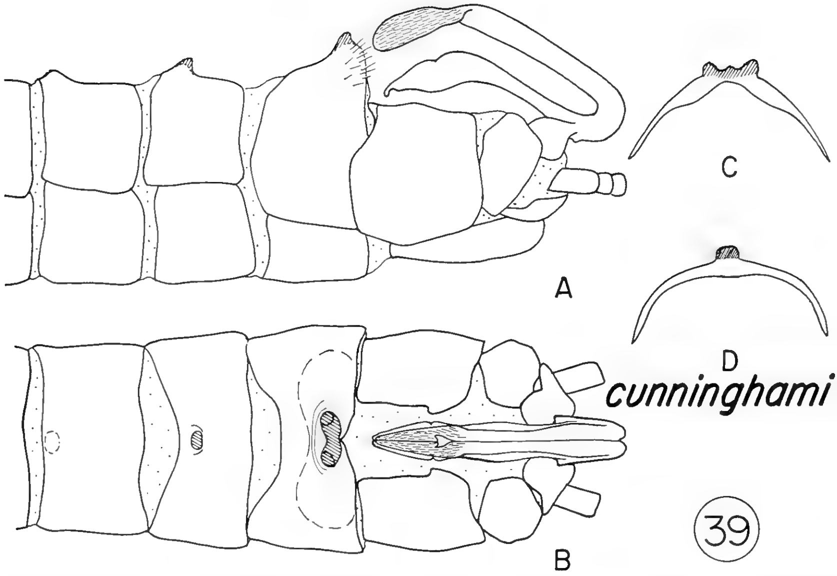
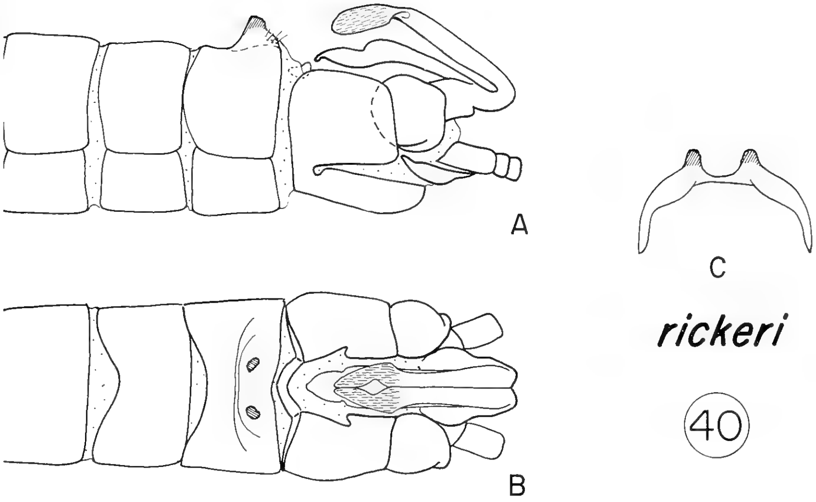
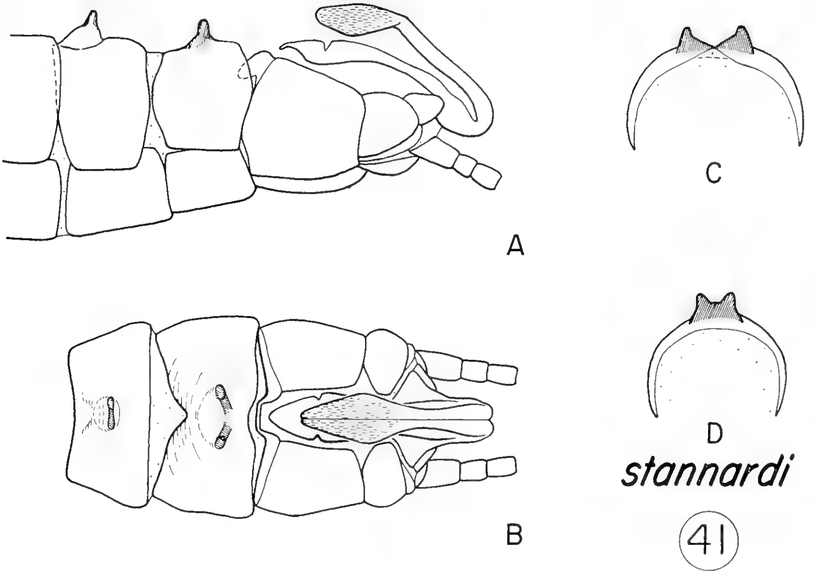


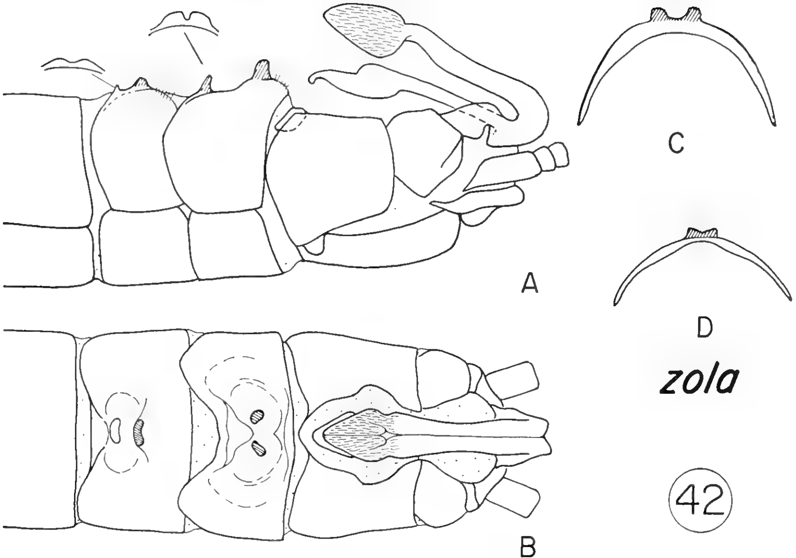
39

FIGS. 38, 39. Terminal abdominal segments of male *Allocapnia sandersoni* and *cunninghami*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.





Figs. 40, 41. Terminal abdominal segments of male *Allocapnia rickeri* and *stannardi*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.



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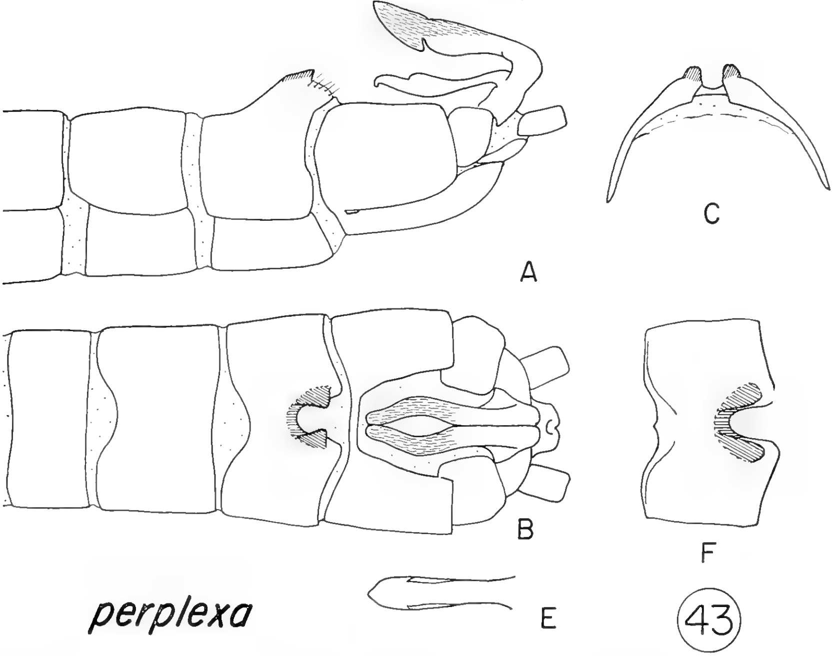
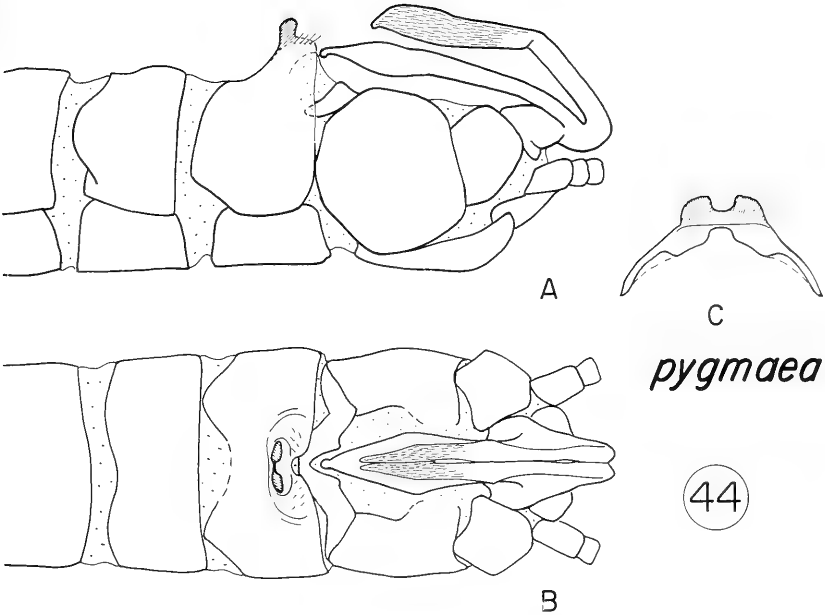
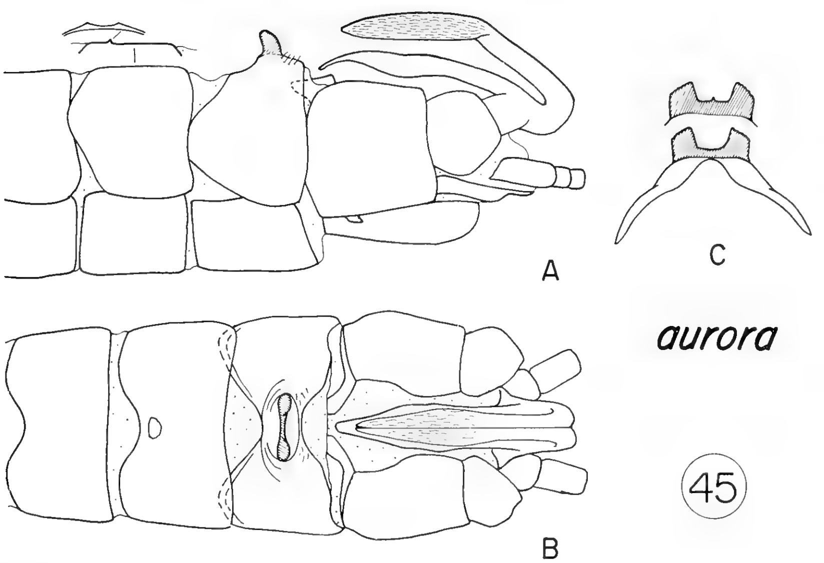


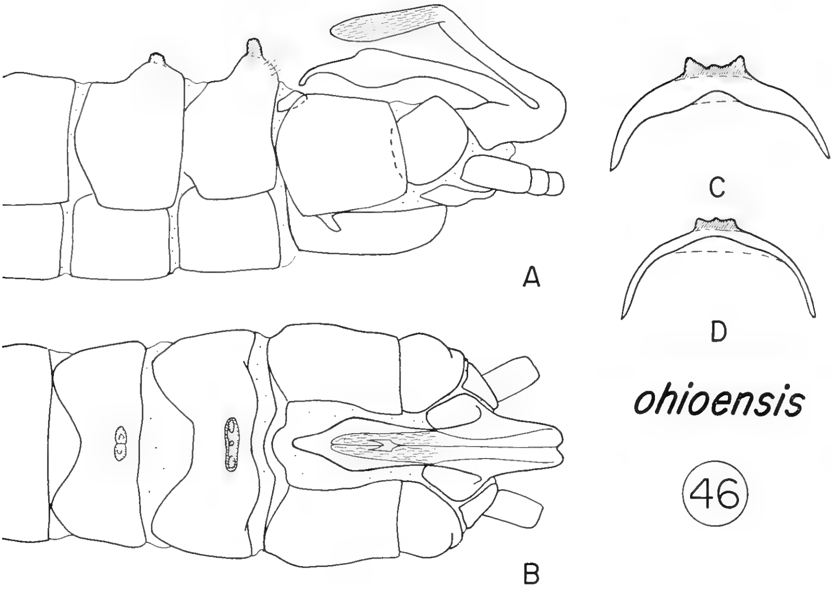
43

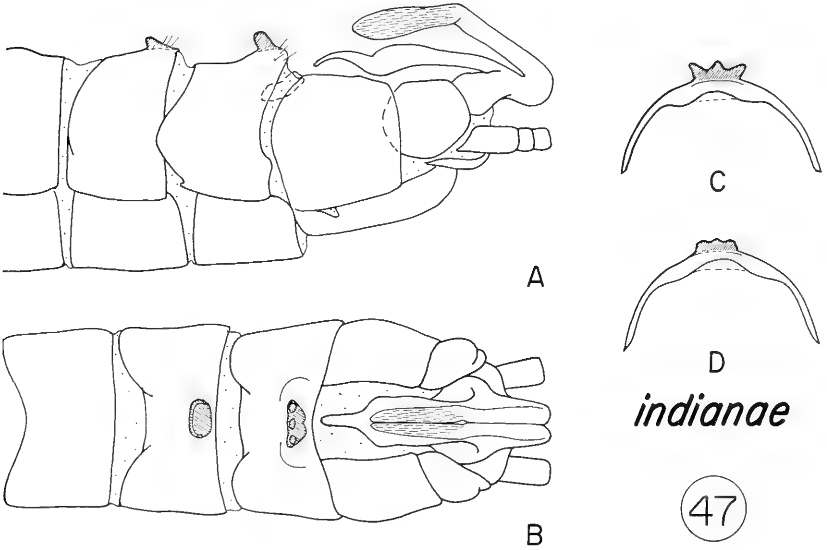
Figs. 42, 43. Terminal abdominal segments of male *Allocapnia zola* and *perplexa*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite; *E*, dorsal aspect of lower limb of epiproct (normally hidden under upper limb); *F*, dorsal aspect of variant eighth tergite.



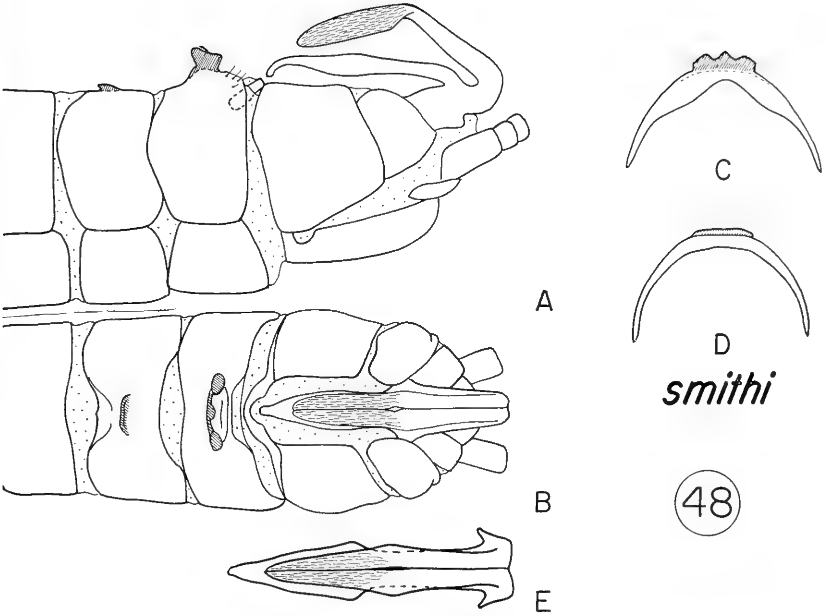


FIGS. 44, 45. Terminal abdominal segments of male *Allocapnia pygmaea* and *aurora*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite, showing two variants (see text).





Figs. 46, 47. Terminal abdominal segments of male *Allocapnia ohioensis* and *indianae*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite.



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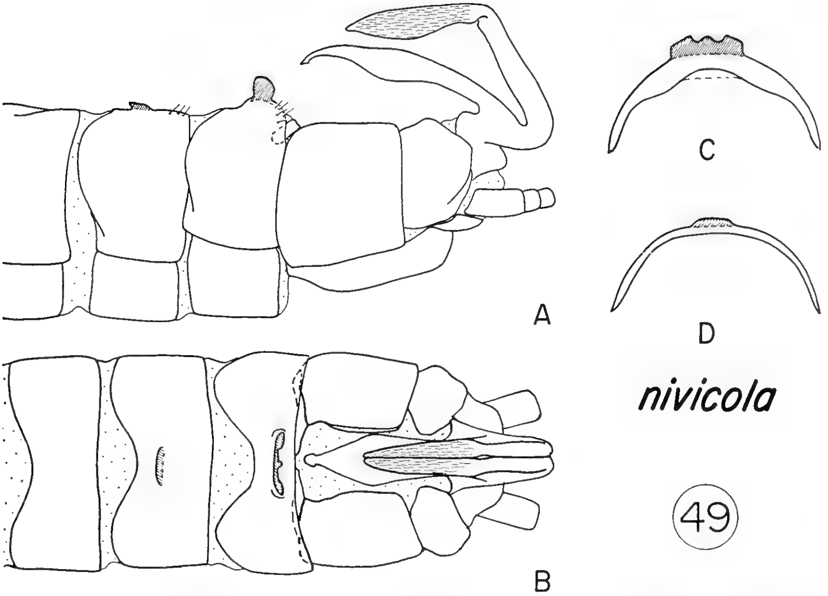

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FIGS. 48, 49. Terminal abdominal segments of male *Allocapnia smithi* and *nivicola*. *A*, lateral aspect; *B*, dorsal aspect; *C*, posterior aspect of dorsal process of eighth tergite; *D*, posterior aspect of dorsal hump of seventh tergite; *E*, variant of epiproct, dorsal aspect.

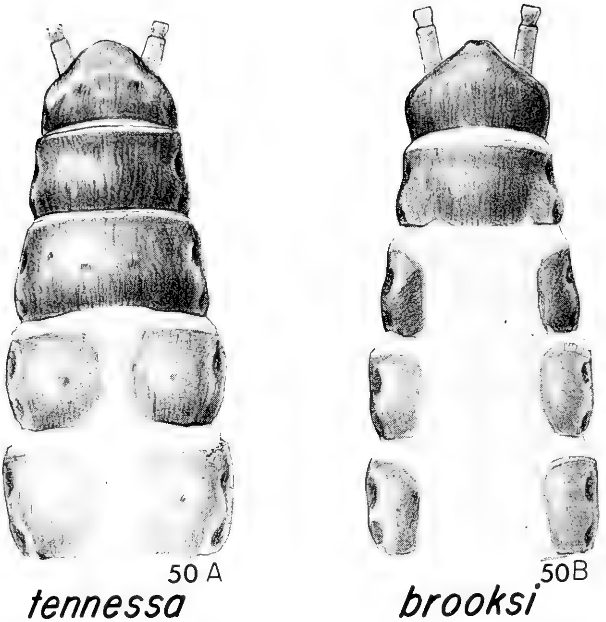
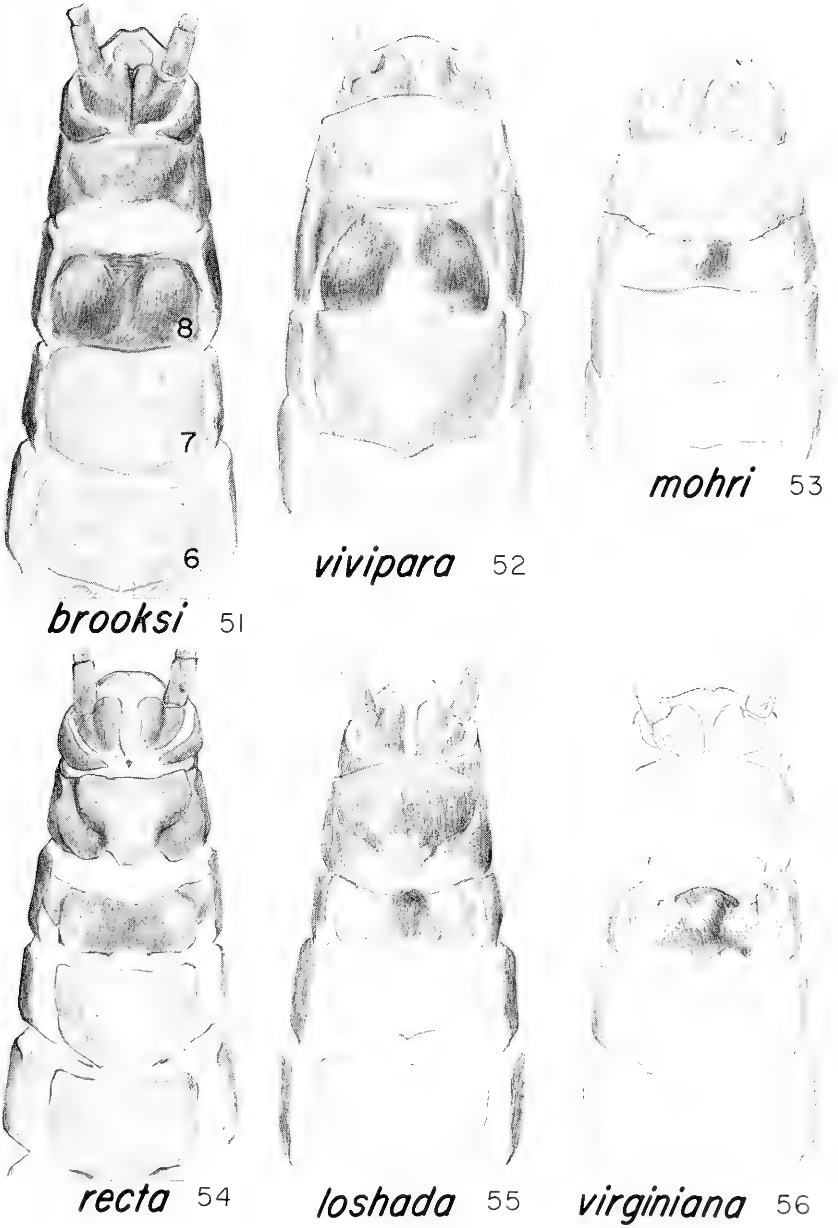
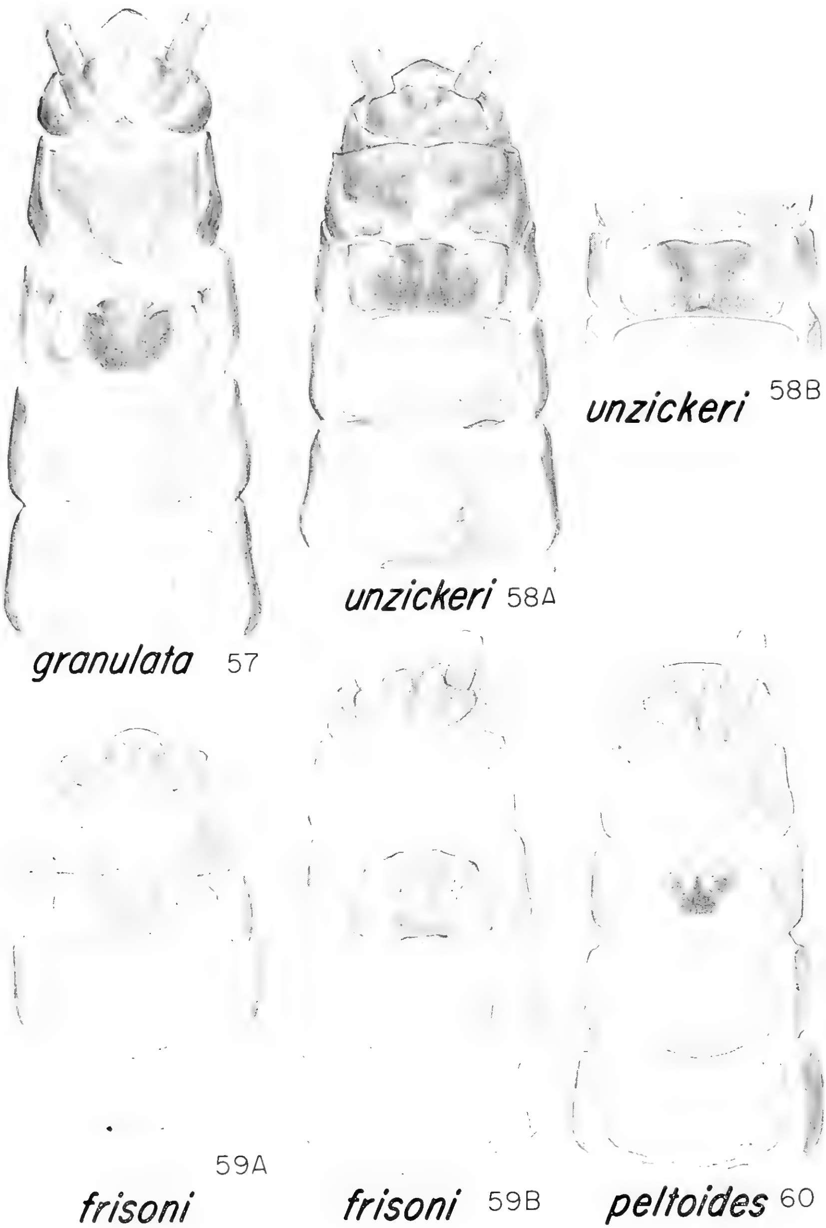


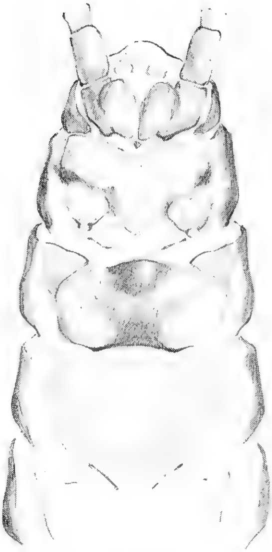
FIG. 50. Apical tergites of female *Allocapnia*. A, *tennessa;* B, *brooksi.*

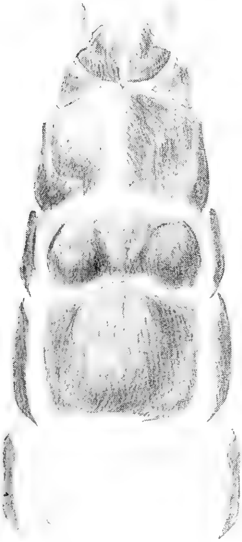


Figs. 51-56. Apical sternites of female *Allocapnia*. 51, *brooksi;* 52, *vivipara;* 53, *mohri;* 54, *recta;* 55, *loshada;* 56, *virginiana*. 6, 7, 8, sternites.

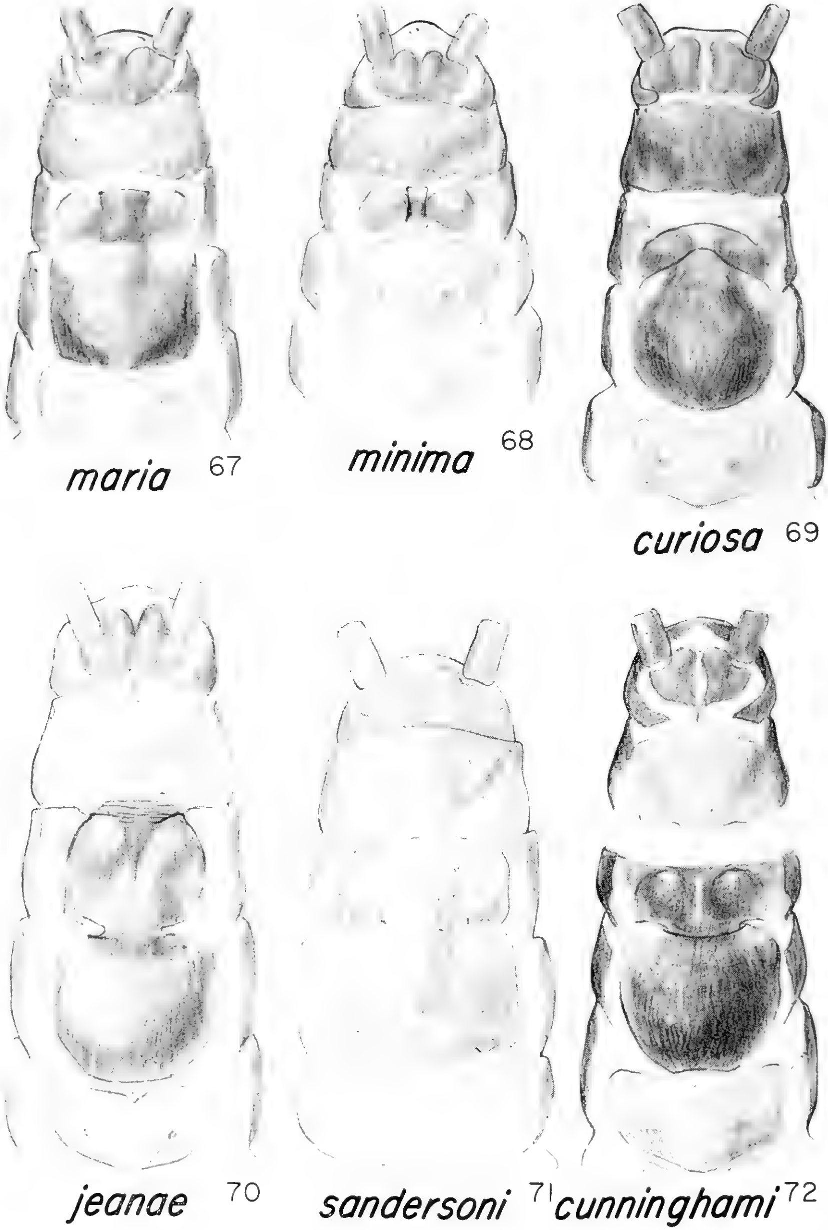


Figs. 57-60. Apical sternites of female *Allocapnia*. 57, *granulata;* 58*A*, *B*, variants of *unzickeri;* 59*A*, *B*, variants of *frisoni;* 60, *peltoides*.

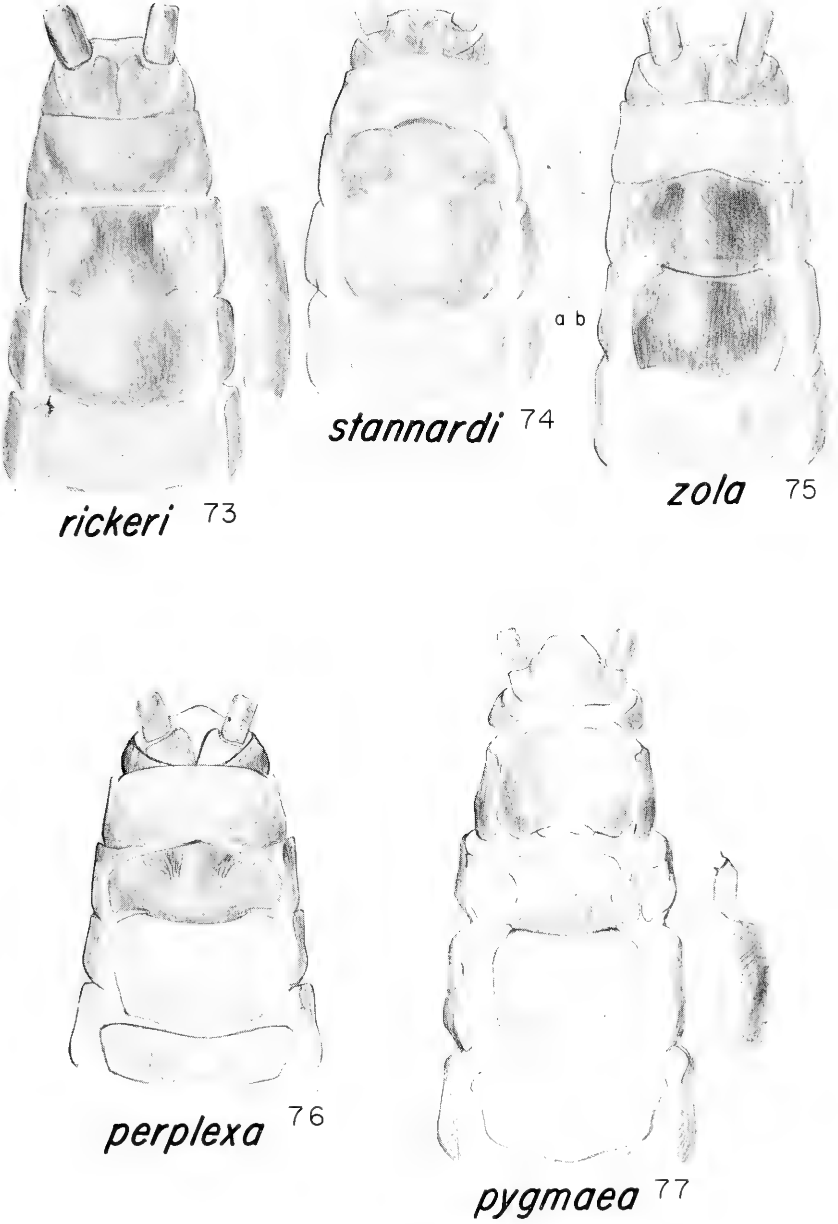




FIGS. 61-66. Apical sternites of female *Allocapnia*. 61, *wrayi*; 62, *mystica*; 63, *illinoensis*; 64, *forbesi*; 65, *ozarkana*; 66, *pechumani*.



FIGS. 67-72. Apical sternites of female *Allocapnia*. 67, *maria;* 68, *minima;* 69, *curiosa;* 70, *jeanae;* 71, *sandersoni;* 72, *cunninghami.*



rickeri 73

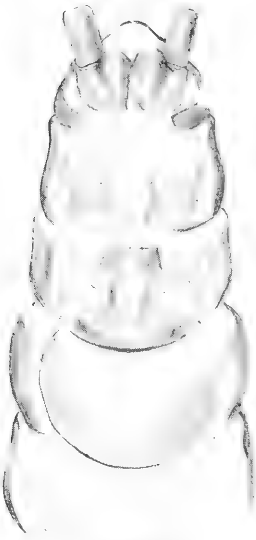
stannardi 74

zola 75

perplexa 76

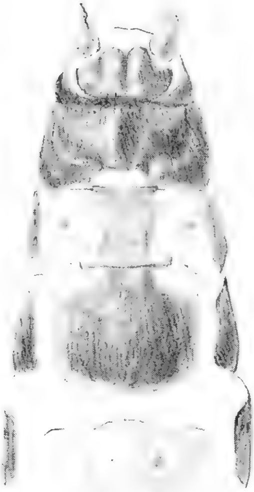
pygmaea 77

FIGS. 73-77. Apical sternites of female *Allocapnia*. 73, *rickeri*; 74, *stannardi*; 75, *zola*; 76, *perplexa*; 77, *pygmaea*. Inset at side, profile of seventh and eighth sternites.



aurora 78

ohioensis 79



indianae 80

indianae 81

smithi 82

nivicola 83

Figs. 78-83. Apical sternites of female *Allocapnia*. 78, *aurora;* 79, *ohioensis;* 80, 81, variants of *indianae;* 82, *smithi;* 83, *nivicola.*

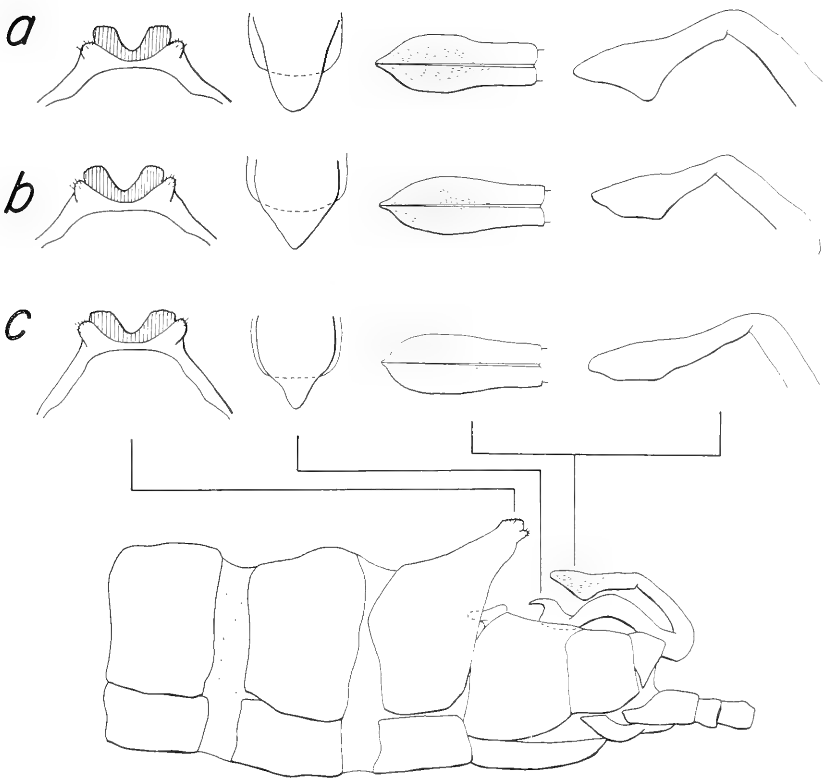


FIG. 84. Male genitalia of *Allocapnia granulata*. Upper row (*a*), typical of eastern populations; lowest row (*c*), typical of Ozark-Ouachita populations; middle row (*b*), intermediate type. (From Ross and Yamamoto, 1967.)

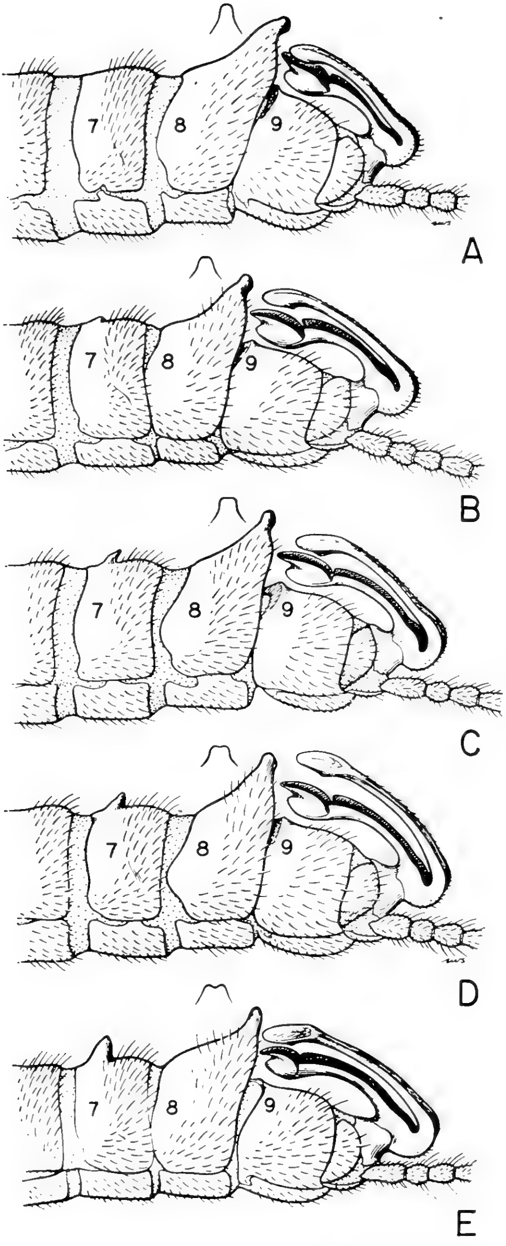


Fig. 85. Terminal abdominal segments of *Allocapnia minima* (A), *maria* (E), and three apparent hybrids (B, C, D). (From Hanson, 1960.)

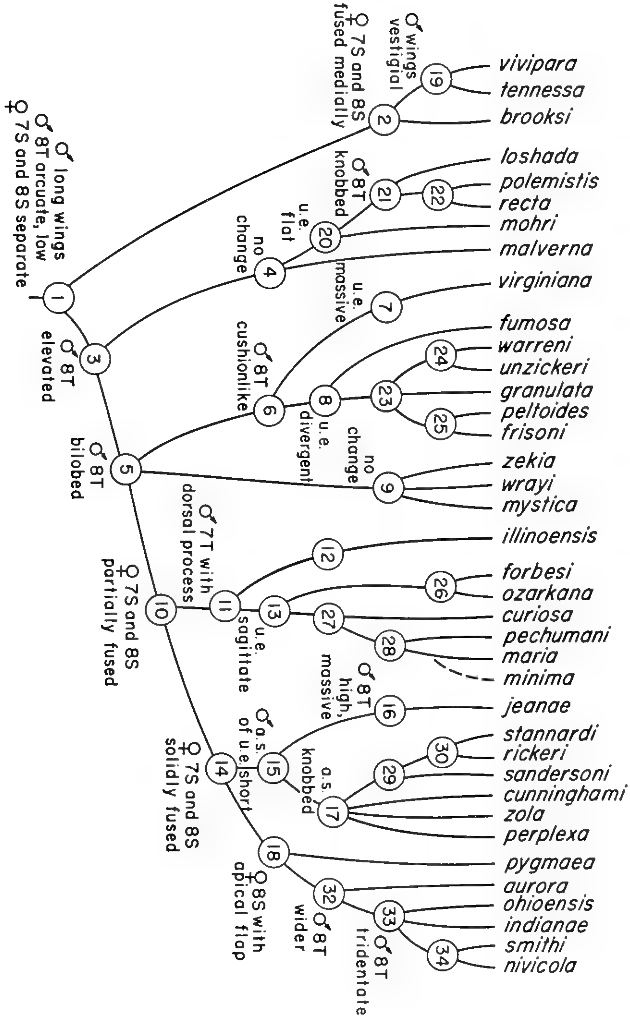


Fig. 86. Phylogenetic chart of *Allocapnia*. Numbers refer to hypothetical ancestral species explained in the text (number 31 not used).

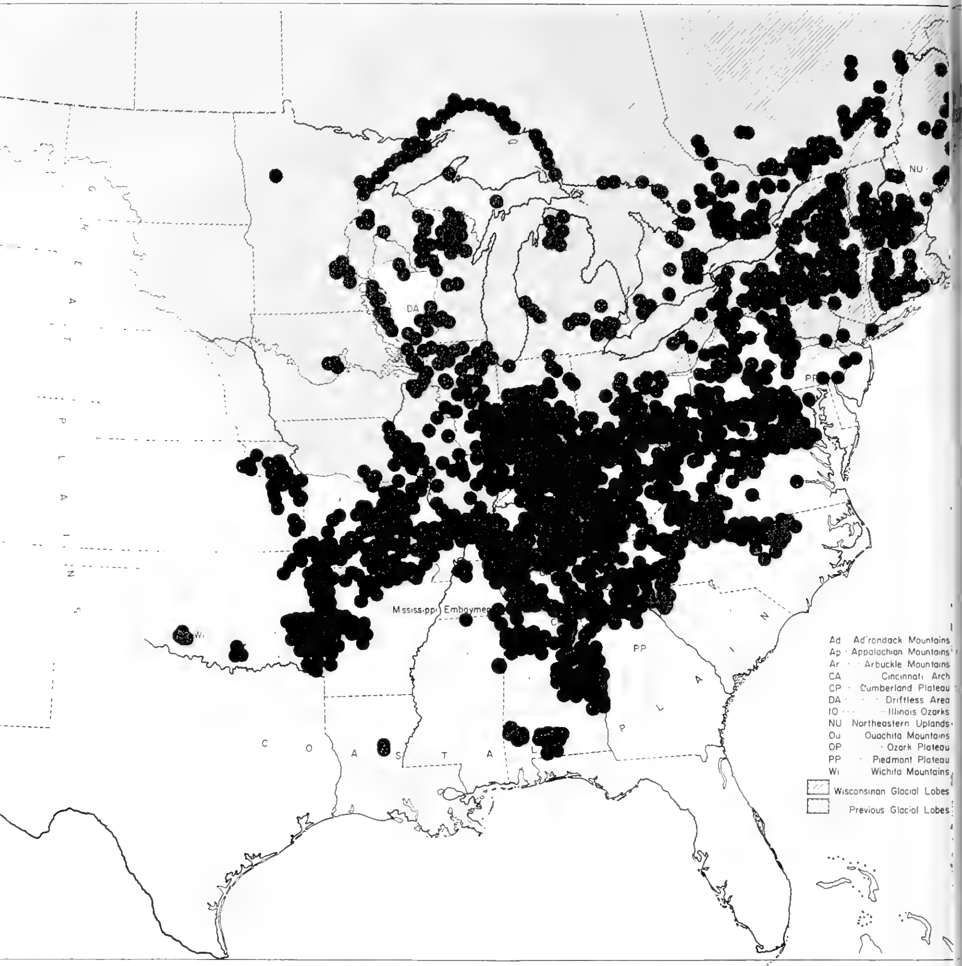


FIG. 87. The bulk of the distribution records for all species of *Allocapnia*. Negative records are not shown, including many localities at which other genera of winter stoneflies were collected, west through South Dakota and southwest to Brownsville, Texas. For more northern and eastern records, see Figs. 99 and 100.

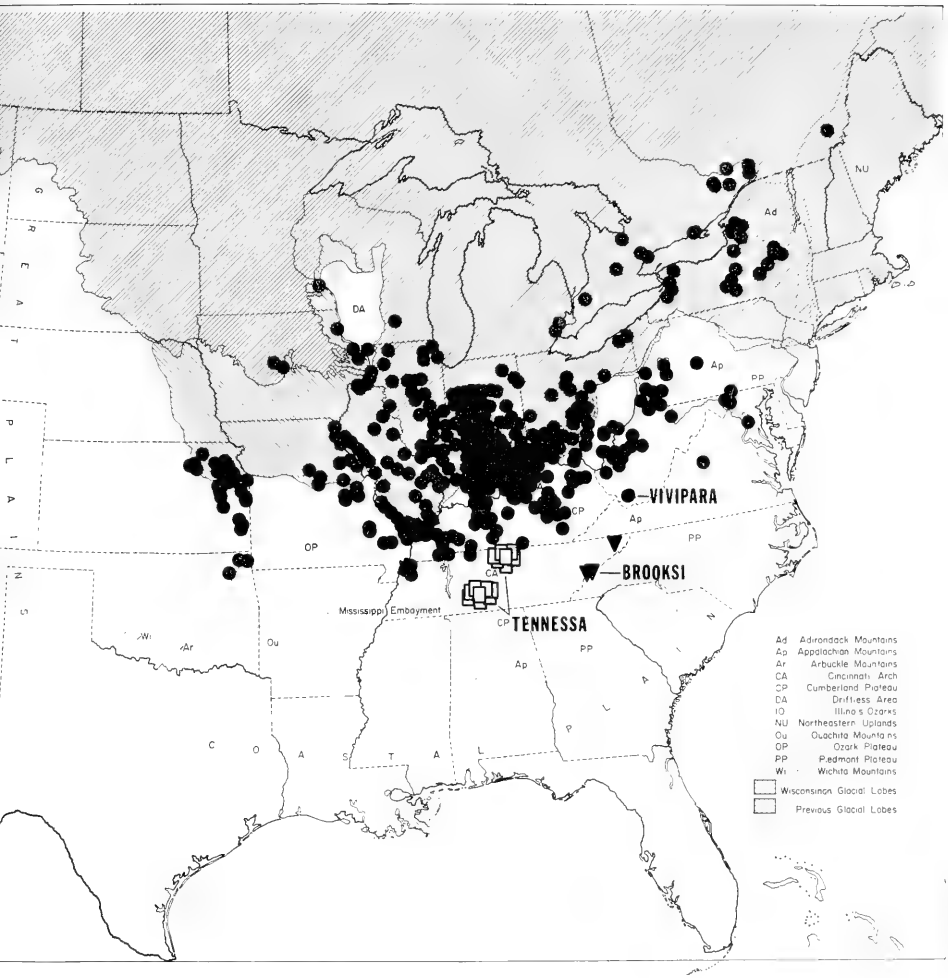


FIG. 88. Distribution of the *Allocapnia vivipara* group.

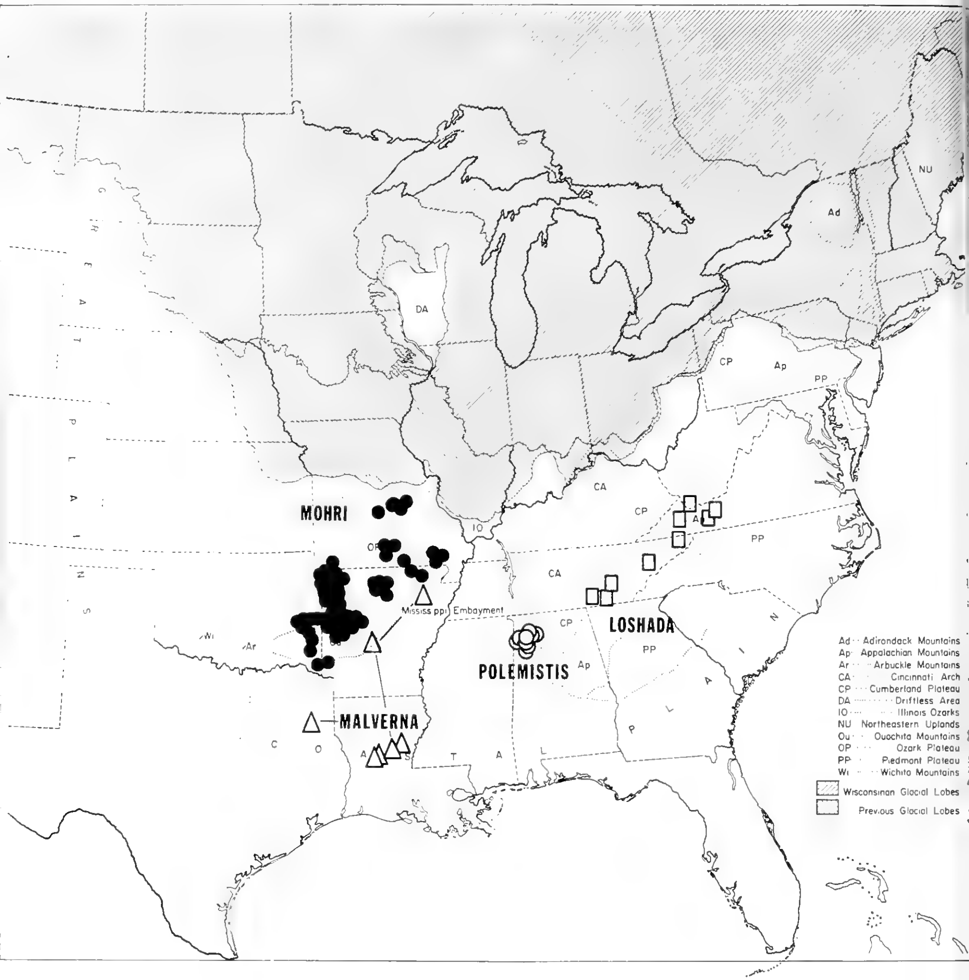


FIG. 89. Distribution of the *Allocapnia recta* group except for *recta*.

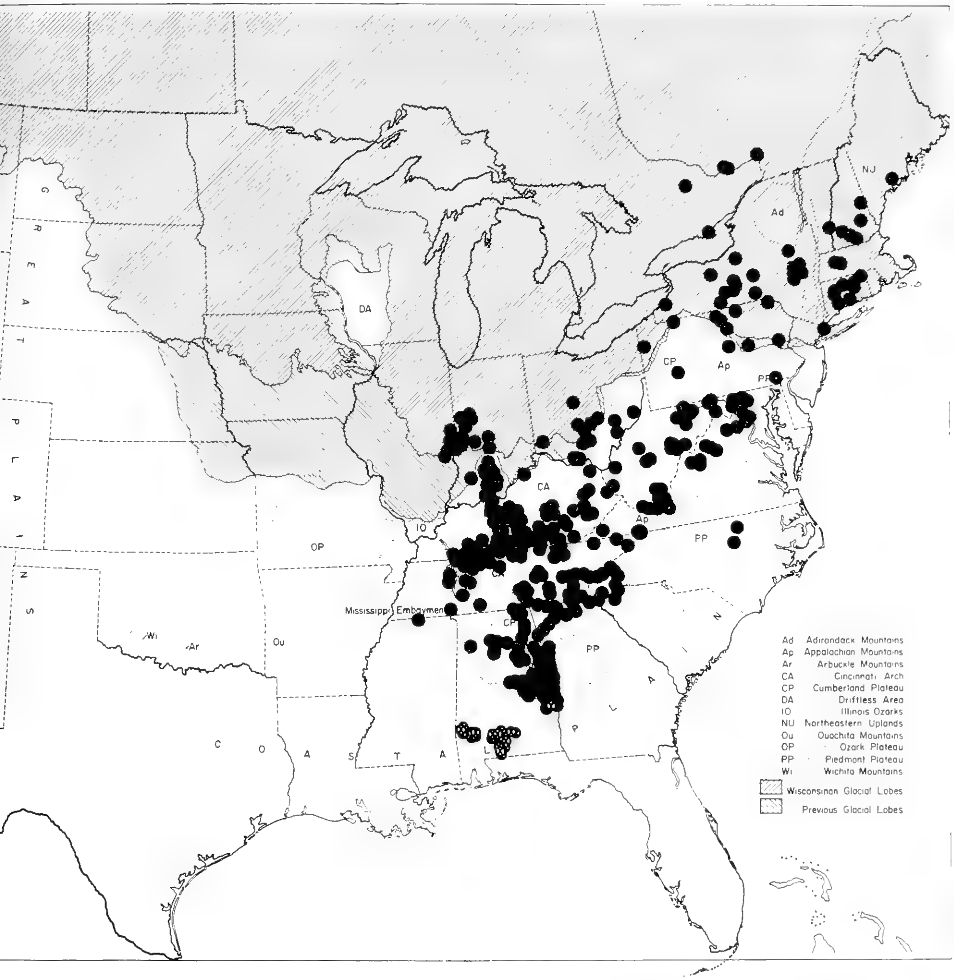


FIG. 90. Distribution of *Allocapnia recta*. Circles with crosses are hybrid flocks of ancestral and derived forms, solid circles are the derived form only.

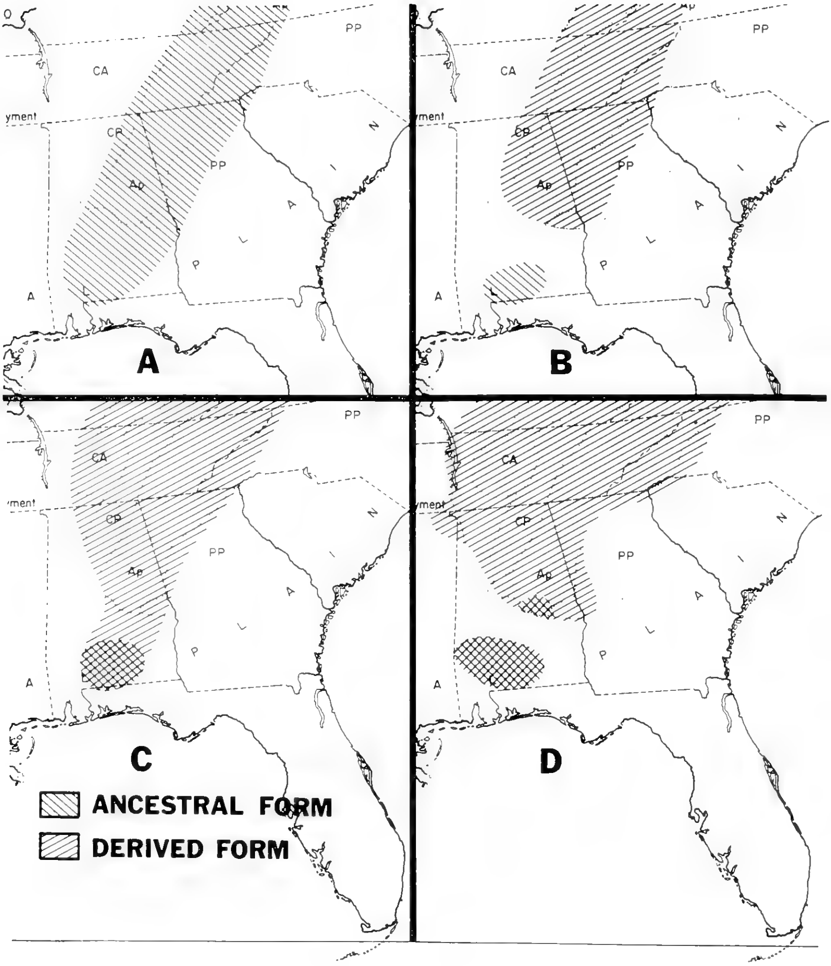


FIG. 91. Postulated stages in the evolution and dispersal of the ancestral and derived forms of *Allocapnia recta* (see also Table p. 62). For explanation, see text (p. 63).

FIG. 92. Distribution of *Allocapnia virginiana*.

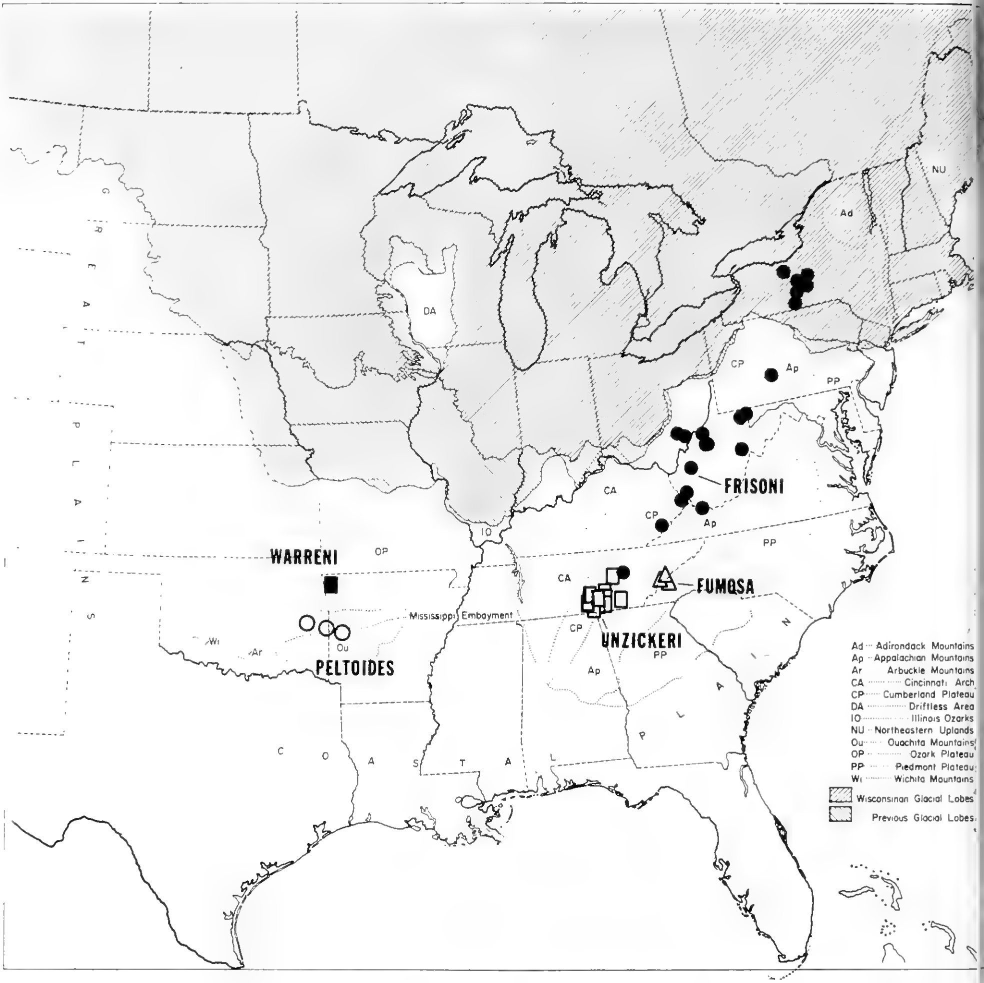


FIG. 93. Distribution of the *Allocapnia granulata* group except for *granulata.*

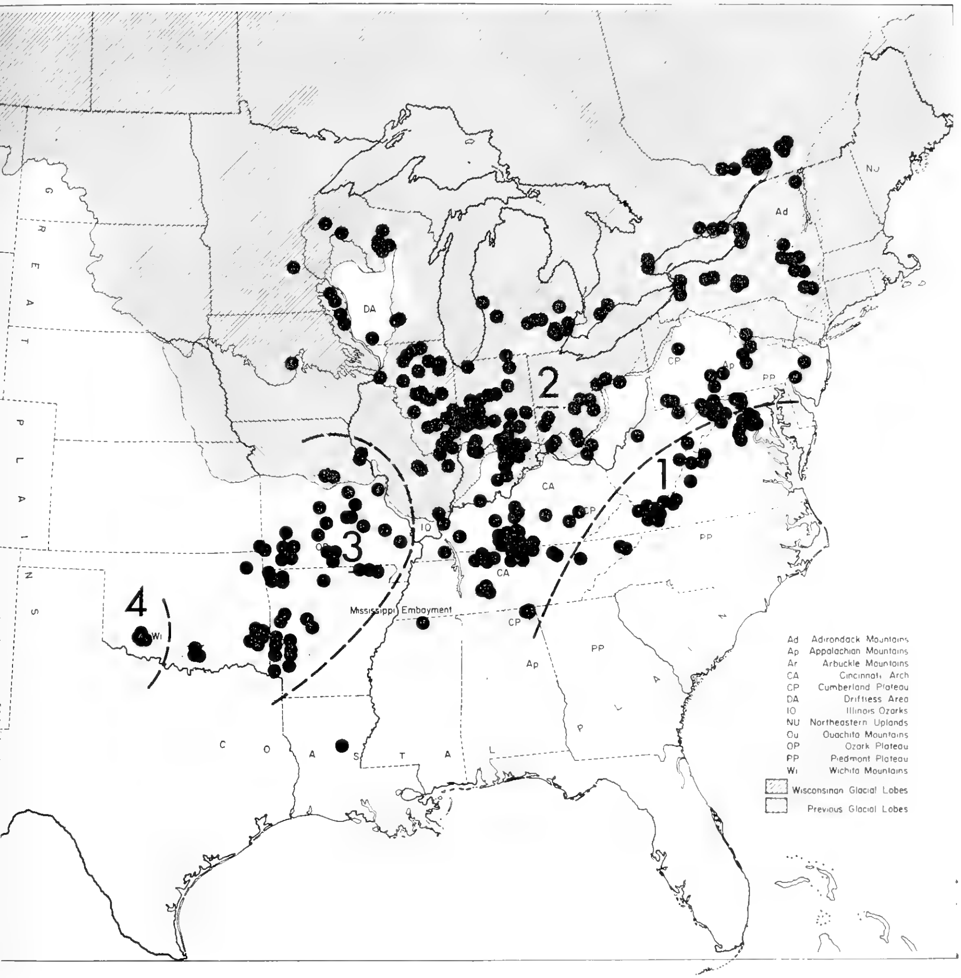


FIG. 94. Distribution of *Allocapnia granulata*. For explanation of numbers, see text (pp. 29-30) and Fig. 95.

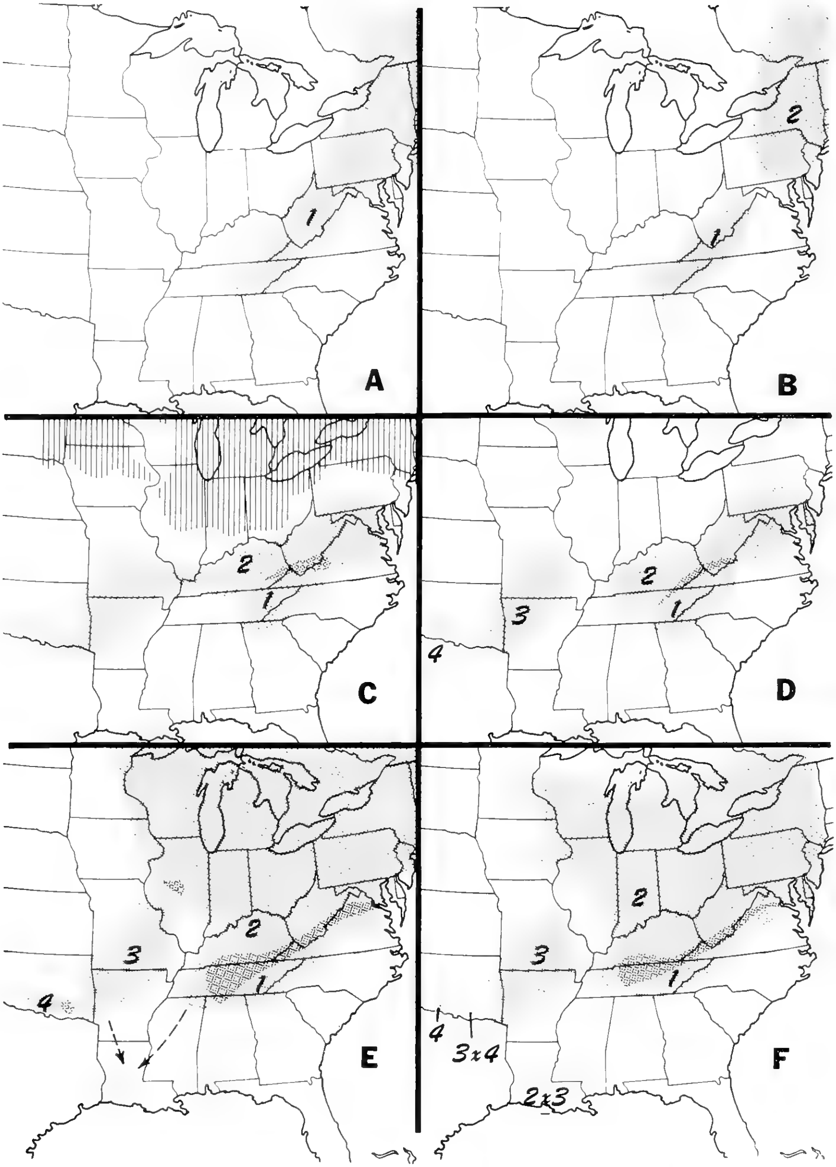


Fig. 95. Postulated stages in the evolution and dispersal of the four populations of *Allocapnia granulata* (see Fig. 94). For explanation, see text (pp. 29-30, 64-65).

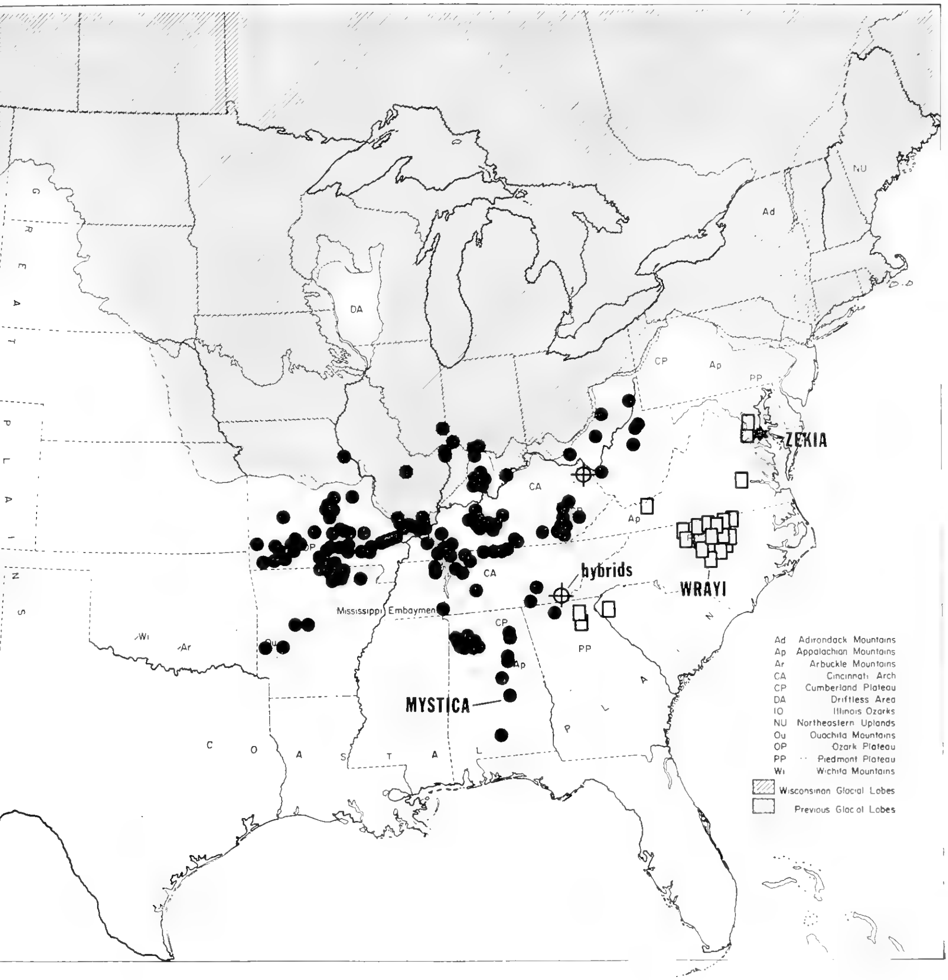


FIG. 96. Distribution of the *Allocapnia mystica* group.

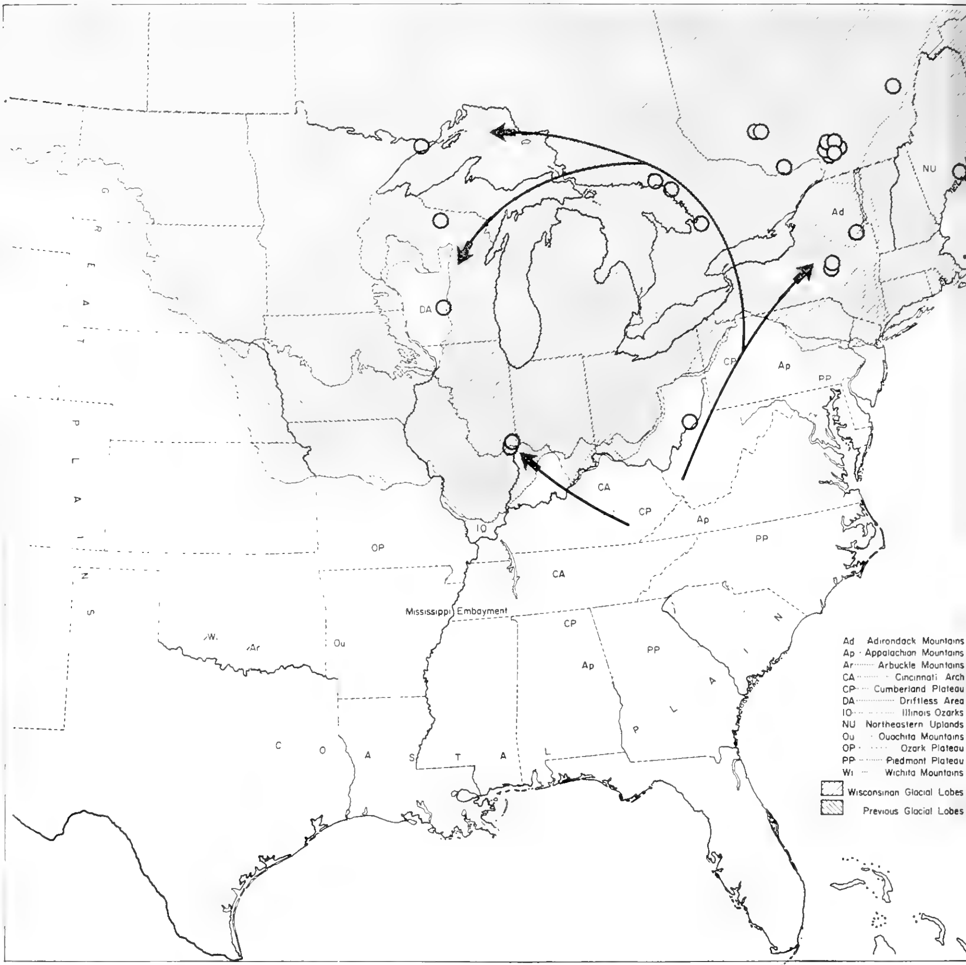


FIG. 97. Distribution of *Allocapnia illinoensis*. Arrows indicate probable post-Pleistocene dispersals.

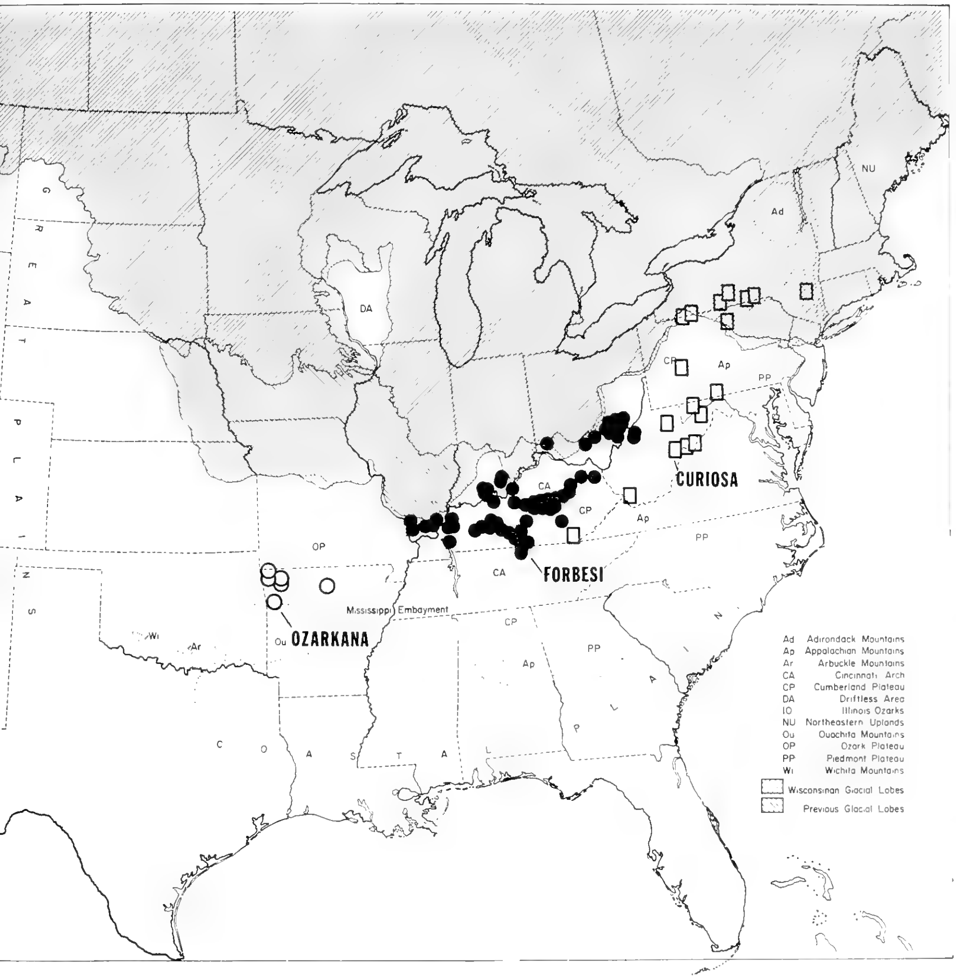


FIG. 98. Distribution of *Allocapnia curiosa*, *forbesi*, and *ozarkana*.

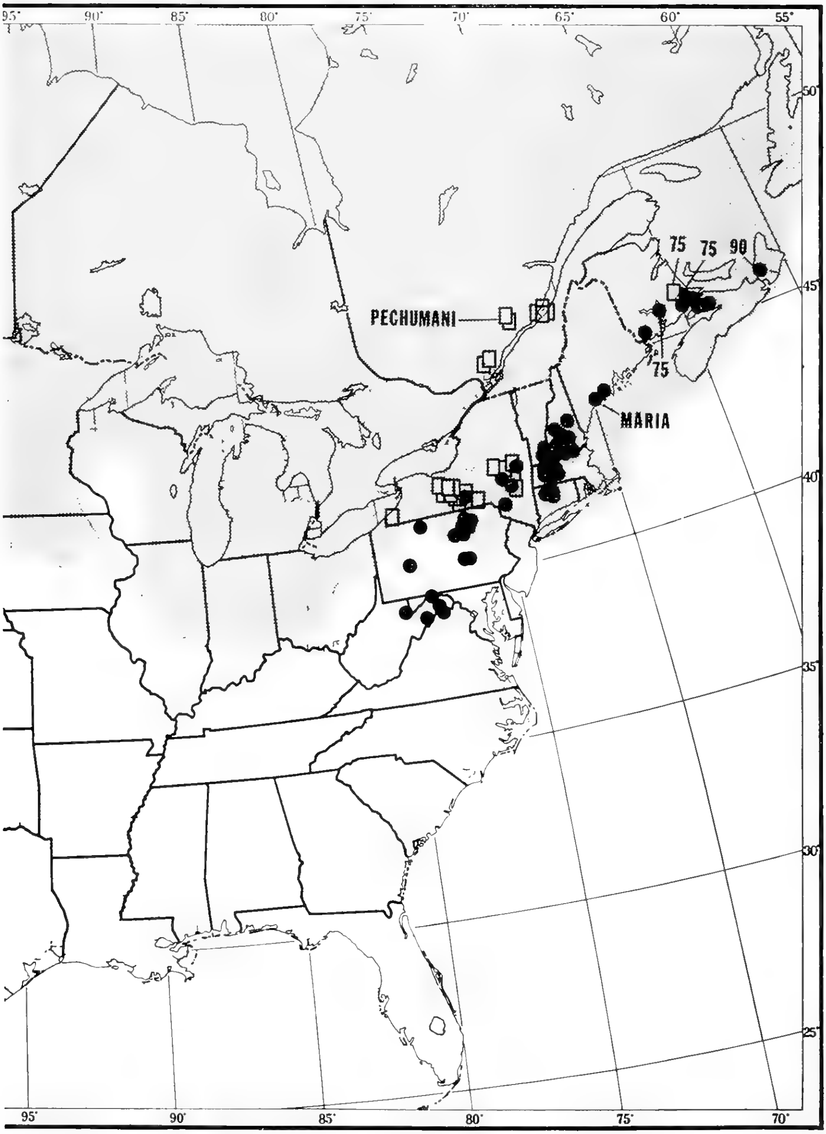


FIG. 99. Distribution of *Allocapnia maria* and *pechumani*. Hybrid populations are denoted by a number, representing an approximation of the percentage of genetic preponderance of the species indicated by the symbol.

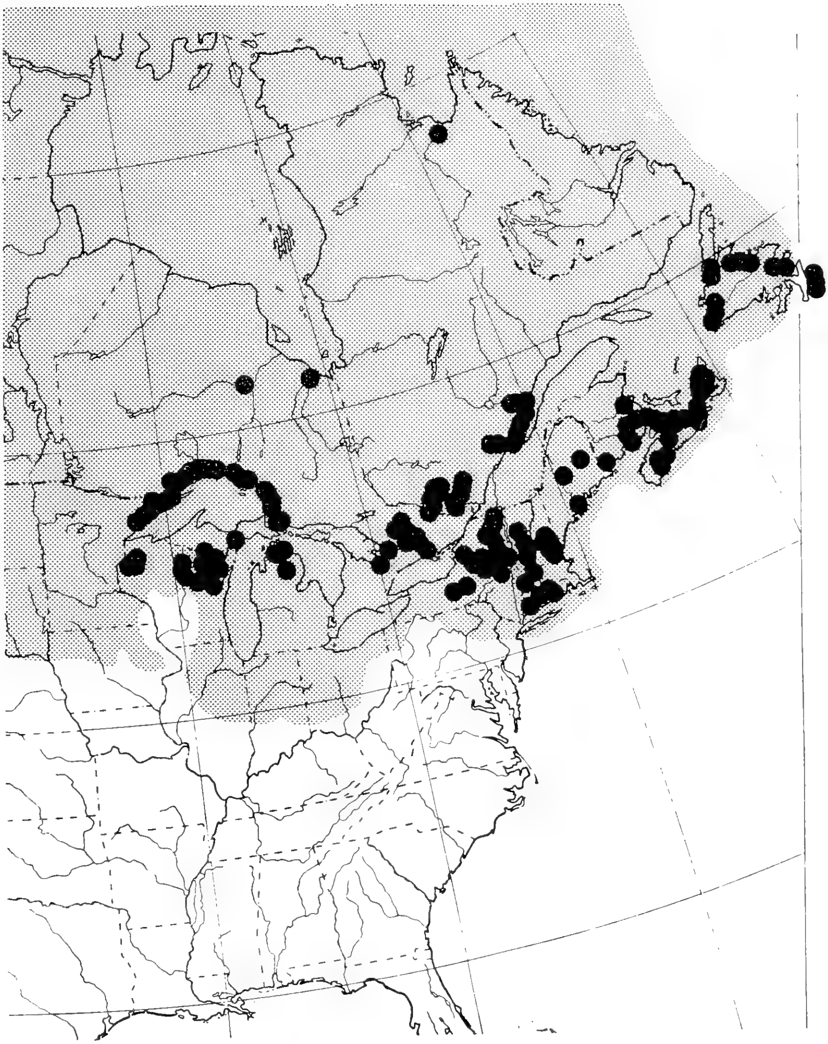


Fig. 100. Distribution of *Allocapnia minima*.

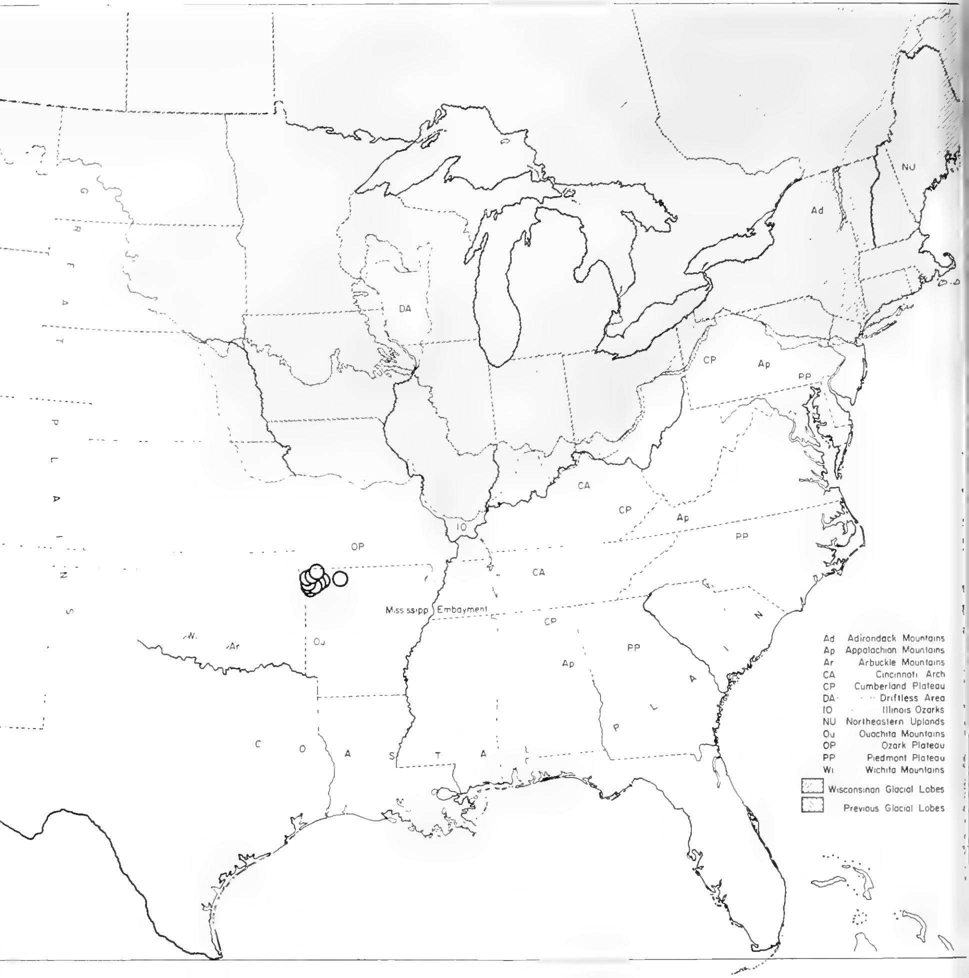


FIG. 101. Distribution of *Allocapnia jeanae*.

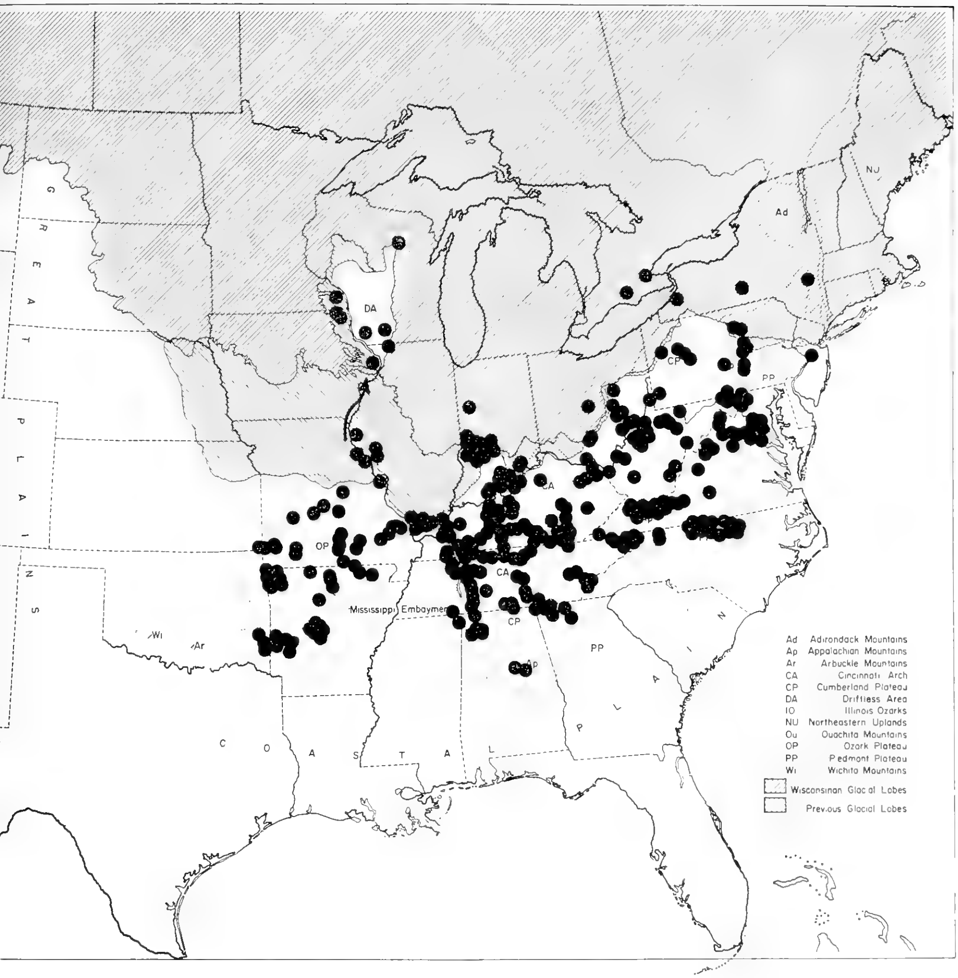


FIG. 102. Distribution of *Allocapnia rickeri*.

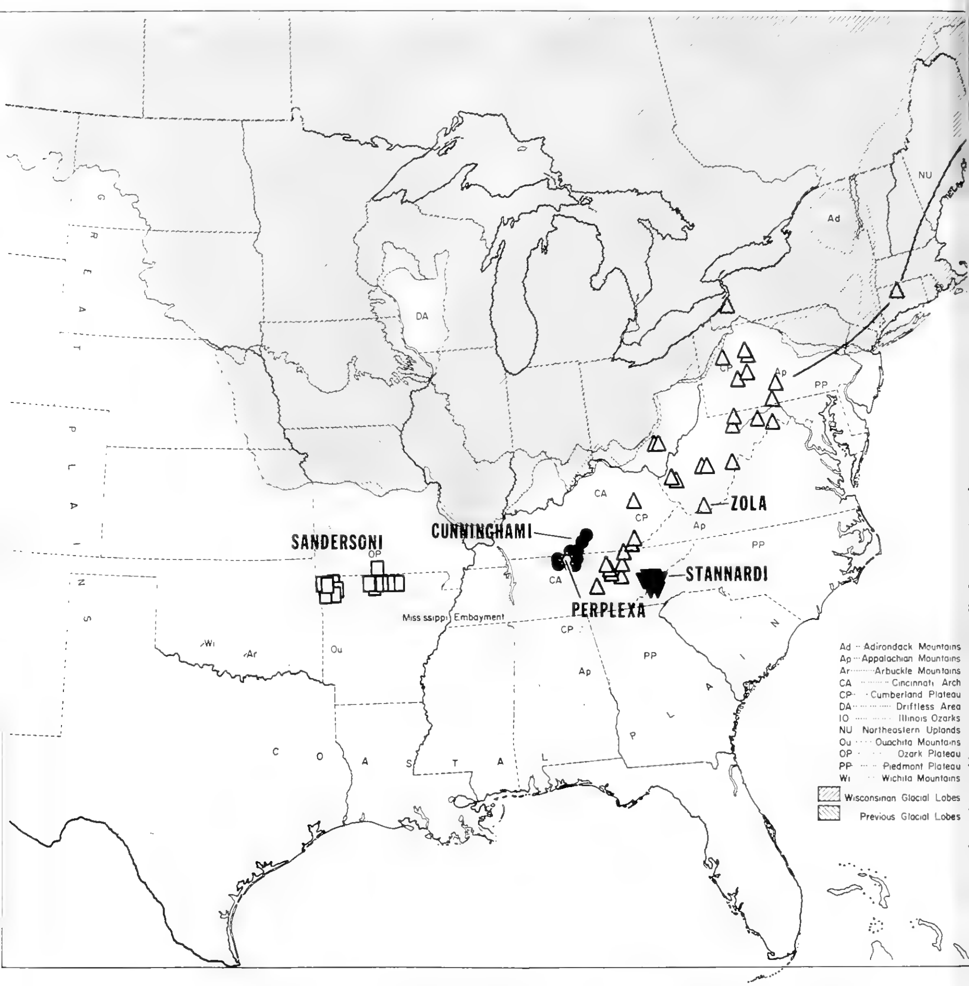


Fig. 103. Distribution of other members of *Allocapnia rickeri* group. The record for *perplexa* is the light area in the middle of the dots for *cunninghami*.

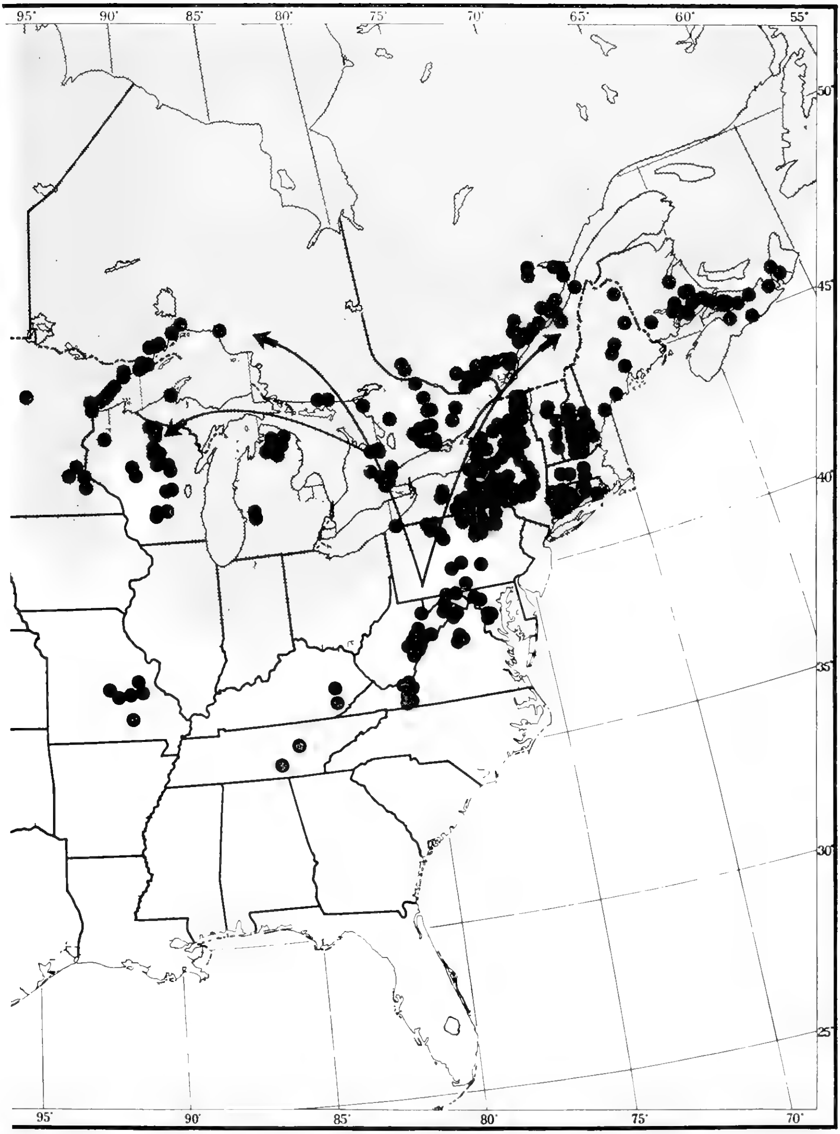


Fig. 104. Distribution of *Allocapnia pygmaea*. Arrows indicate probable routes of post-Pleistocene dispersal.

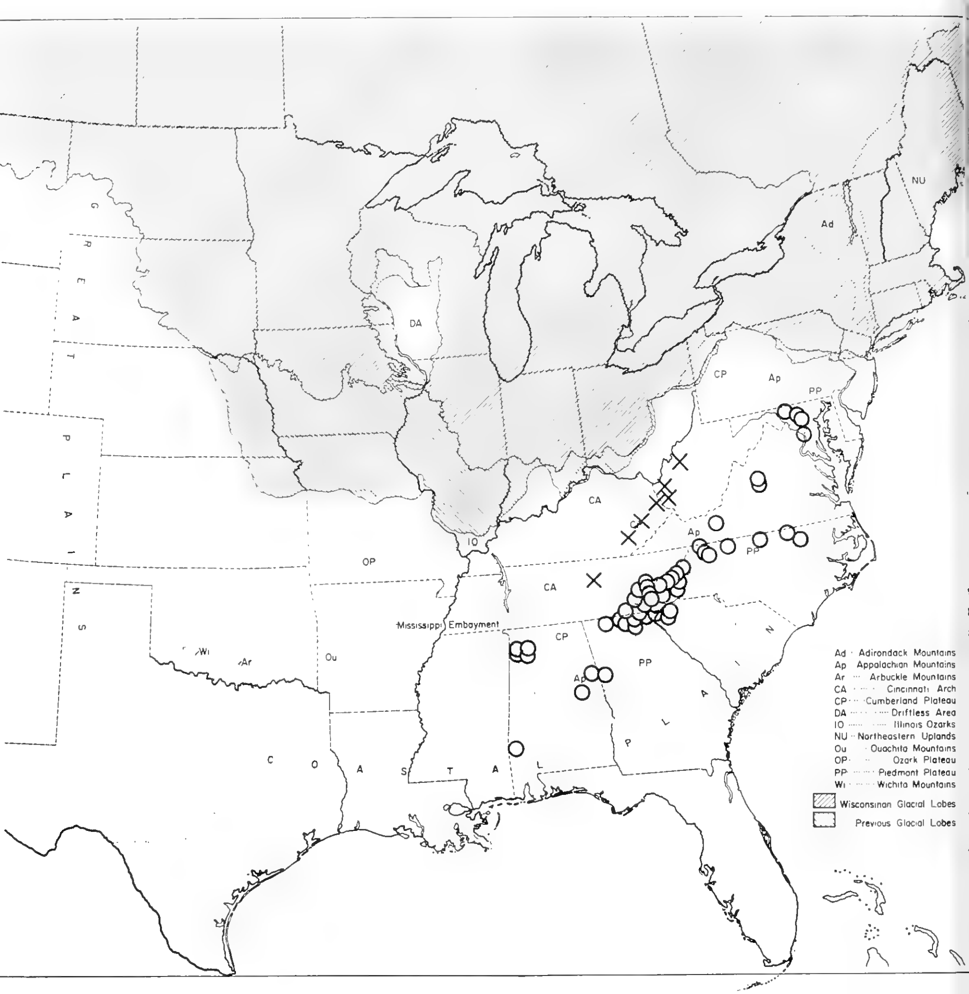


FIG. 105. Distribution of *Allocapnia aurora* (open circle). The "x" 's are populations of *nivicola* having possible *aurora* x *nivicola* hybrids.

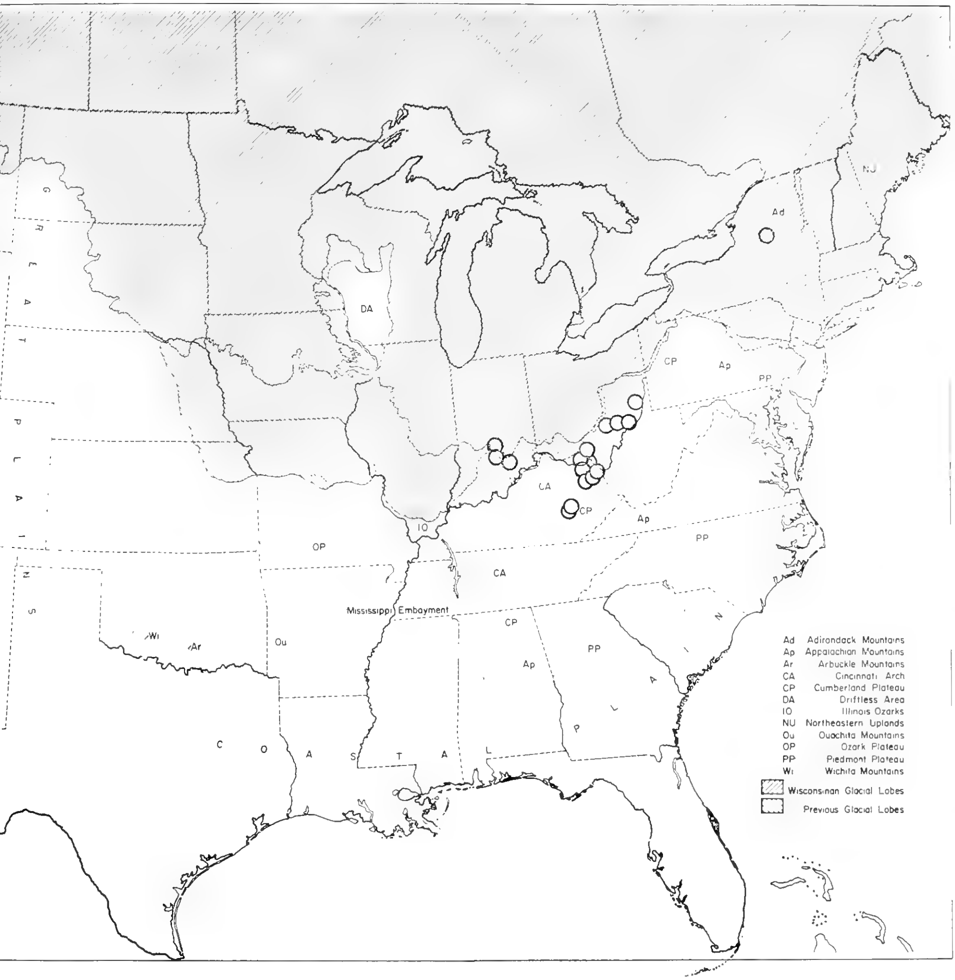


FIG. 106. Distribution of *Allocapnia ohioensis*.

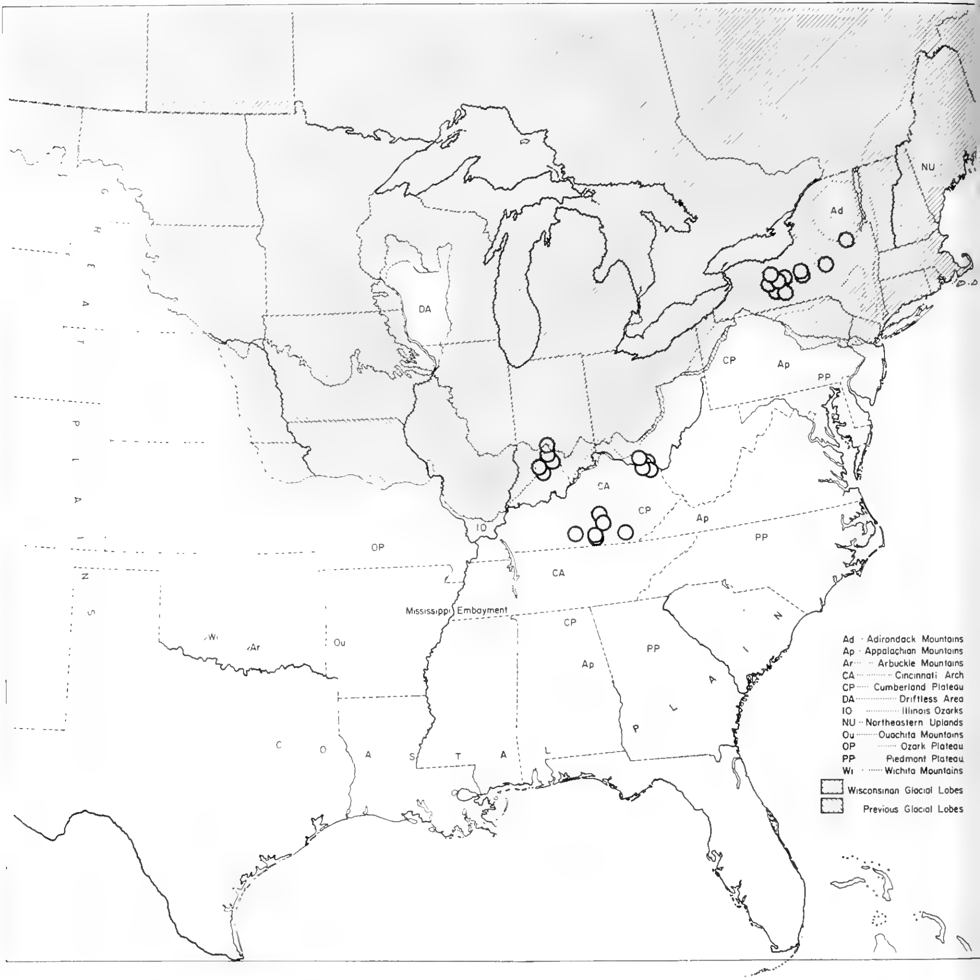


FIG. 107. Distribution of *Allocapnia indianae*.

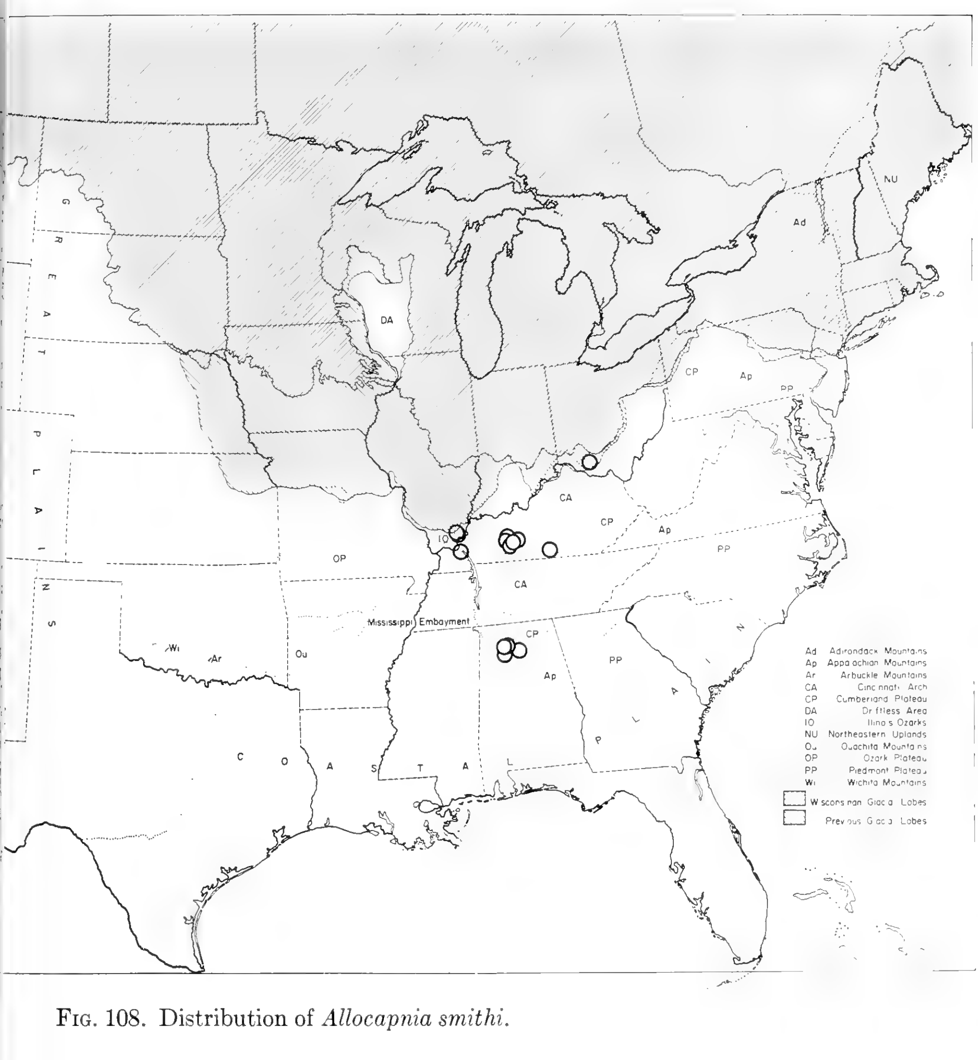


FIG. 108. Distribution of *Allocapnia smithi*.

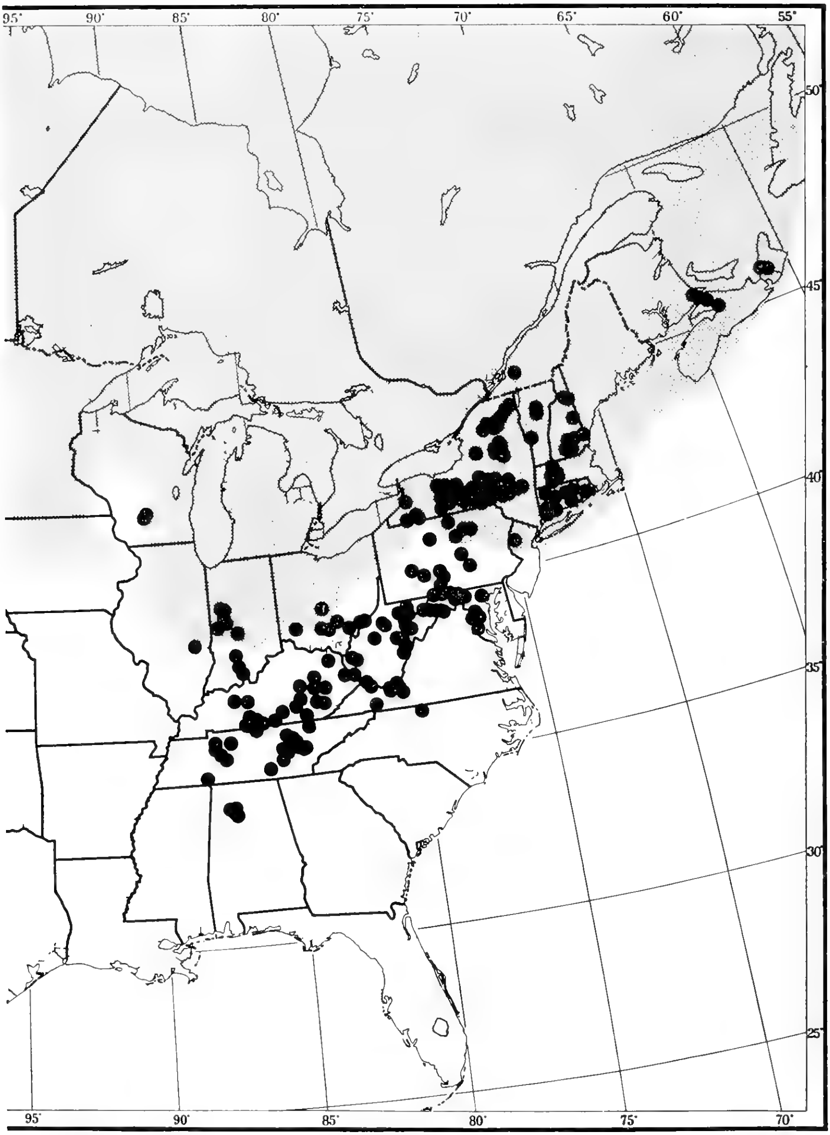
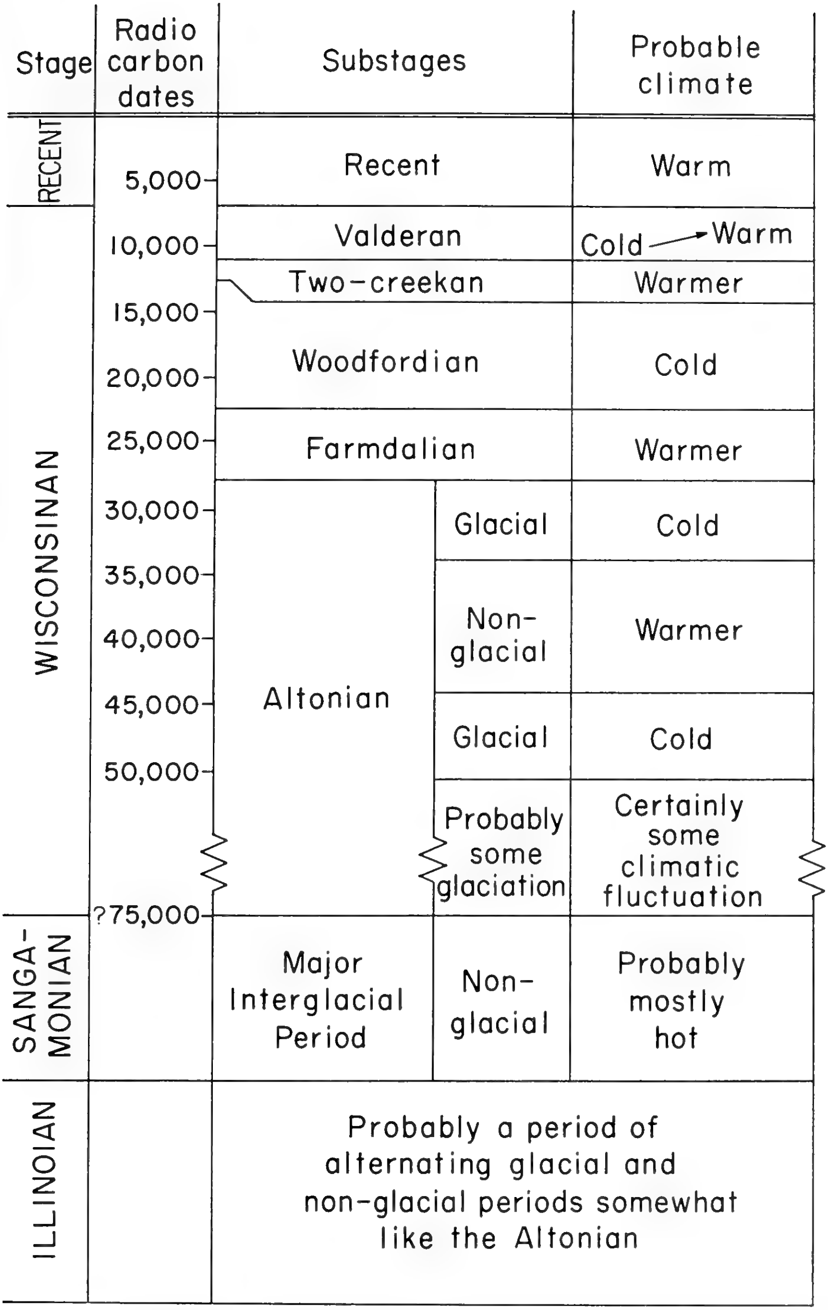


Fig. 109. Distribution of *Allocapnia nivicola*.



Stage	Radio carbon dates	Substages		Probable climate
RECENT	5,000	Recent		Warm
WISCONSINAN	10,000	Valderan		Cold → Warm
		Two-creekan		Warmer
	15,000 20,000	Woodfordian		Cold
	25,000	Farmdalian		Warmer
	30,000	Altonian	Glacial	Cold
	35,000 40,000		Non-glacial	Warmer
	45,000		Glacial	Cold
	50,000		Probably some glaciation	Certainly some climatic fluctuation
SANGAMONIAN	?75,000	Major Interglacial Period	Non-glacial	Probably mostly hot
ILLINOIAN		Probably a period of alternating glacial and non-glacial periods somewhat like the Altonian		

Fig. 110. Generalized climates in eastern and central United States during the substages of the Wisconsinan stage of the Pleistocene. (Adopted from Frye et al., 1969.)

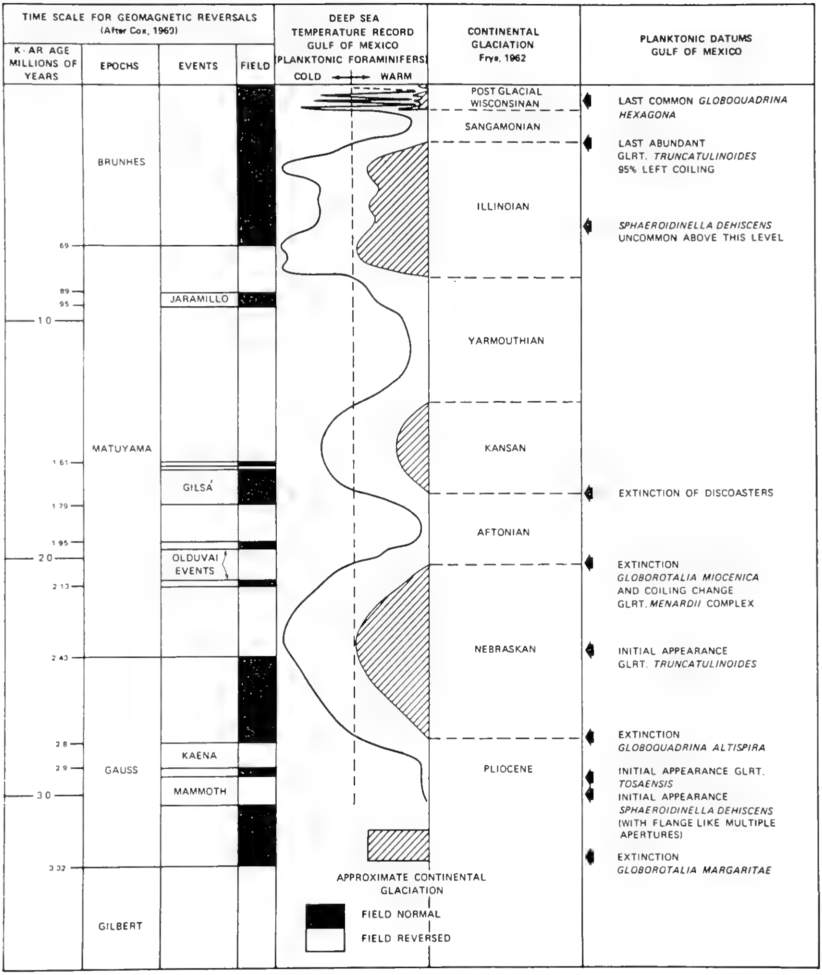


FIG. 111. A summary of pertinent features concerning dating, climates, and name correlations for the Pleistocene and late Pliocene in southeastern North America, based on planktonic organisms in cores from the Gulf of Mexico. (From Beard, 1969.)

INDEX

Names printed in italics are synonyms. Numbers in italics indicate principal references.

A Note on the Authors

Herbert H. Ross, professor of entomology at the University of Georgia in Athens, formerly was professor of entomology at the University of Illinois and head of the Section of Faunistic Surveys and Assistant Chief of the Illinois Natural History Survey.

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