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BIOLOGY AND IMMATURE STAGES OF MALACOPHAGOUS DIPTERA OF THE GENUS KNUTSONIA VERBEKE (SCIOMYZIDAE) (1)

BY

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INTRODUCTION

The first direct observations of the malacophagous (mollusk-eating) habits of sciomyzid larvae were made by Berg (1953), who suggested that the *Sciomyzidae*, « ...may be integrated biologically by the common food preferences of their larvae. » Over 160 of the 500 described species of this acalyptrate family have now been reared, and all have developed from hatching to puparium formation solely on snails, snail eggs, slugs, or fingernail-clams (*Sphaeriidae*). The habits of the larvae in attacking, killing, and feeding in their molluskan prey or hosts form a behavioral continuum, ranging from predaceous to parasitoid. Parasitoid larvae are like parasites, in associating so intimately with the living host that they are able to feed within it for a relatively long time. But unlike parasites, parasitoid larvae inevitably kill the food organism because they must consume major proportions of their victim's bodies to satisfy their own food requirements (Berg, 1964). Associated behavioral and morphological adaptations present throughout the life cycle also show various degrees of complexity.

The most highly specialized parasitoid *Sciomyzidae* feed on terrestrial or hygrophilous snails and all belong to the same major taxonomic category (the Sciomyzinae as used by some authors or Sciomyzini of Steyskal, 1965). Females of these species (*e.g. Sciomyza aristalis* Co-

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QUILLET; FOOTE, 1959) cement an egg onto the shell of a snail for which they have some degree of host specificity. The larva feeds in the less vital tissues of the host for more than a week before killing it and characteristically kills only one snail. After the snail dies, the larva continues to feed in the decomposing tissue for a short time, consuming most of it before pupating. The puparium is formed in the shell on which the egg was laid, and puparia of some species are strangely shaped to fit within.

The aquatic, predaceous end of the behavioral continuum is represented by many species and genera of the other major taxonomic category (the *Tetanocerinae* of previous authors or *Tetanocerini* of STEYSKAL, 1965). Eggs of these species (*e.g. Hydromya dorsalis* (FABRICIUS), KNUTSON and BERG, 1963; *Elgiva* spp., KNUTSON and BERG, 1964; *Sepedon* spp., NEFF and BERG, 1966; and most species of *Knutsonia* VERBEKE treated herein) are laid on emergent vegetation, and the newly-hatched larvae characteristically search for the prey. Little if any host-specificity is shown; species of *Lymnaeidae*, *Physidae*, and *Planorbidae* are attacked indiscriminately. Prey are killed within a few minutes, and the larvae leave after feeding to repletion. Up to 40 snails may be killed and partly eaten during the three stadia of development from egg to pupa. Puparia are formed outside the shell of the food snail and are well adapted for flotation.

Between these two extremes of terrestrial, parasitoid and aquatic, predaceous behavior there are many species belonging to both major taxonomic categories which have intermediate and mixed behavior. Most morphological features of their immature stages also are intermediate between the typical terrestrial and aquatic species. In some (*e.g. Atrichomelina pubera* LOEW; FOOTE *et al.*, 1960) the feeding behavior is extremely variable. Such larvae are capable of predatory, parasitoid, and even saprophagous feeding habits. Others (*e.g. Antichaeta analis* ZETTERSTEDT; KNUTSON, 1966) have a few parasitoid characteristics, such as host-specificity and oviposition on the host, but otherwise they behave as typical predators. A few species (*e.g. Sepedon h. hispanica* LOEW, KNUTSON, *et al.*, in press; *Tetanocera elata* MEIGEN, KNUTSON, *et al.*, 1965) exhibit two rather distinct phases in their life cycles, beginning larval development as covert parasitoids and completing it as overt predators.

The *Sciomyzidae* appear to be an exceptionally favorable group for a study of the evolution of predatory and parasitoid behavior. As indicated in the above sketch, a considerable amount of behavioral information can be obtained from the family. However, that behavior is not so involved that the sheer mass of complex data makes generalization and the determination of relationships extremely difficult. The fact that all biologically known larvae have a basic similarity, *i.e.* feeding on mollusks, makes comparisons of species easier and more significant. Closely associated with these favorable levels of complexity and diversity of behavior is the favorable size of the family. With about 500 species in about 60 genera, there is a greater probability of being able to study the biology of a large percentage of this family than there is for other, much larger, groups of predaceous and parasitoid insects. Speculation on the evolution of a group should more closely approach reality as the percentage of its studied species increases. Furthermore, with the *Sciomyzidae* one can utilize the unique information that is gained by studying related organisms in different geographical regions. The *Sciomyzidae* have a predominantly northern hemisphere distribution, but there are also rather well developed Neotropical and Ethiopian elements. The high percentage of the world fauna which is described, availability of keys, and other basic, taxonomic aspects are, of course, fundamental for the development of this type of study. Due to the extensive studies of J. VERBEKE (Brussels), G. C. STEYSKAL (Washington), and other investigators, the taxonomy of the *Sciomyzidae* is becoming well known for most regions.

Several characteristics of a practical nature contribute importantly to the relative ease of working with the *Sciomyzidae*. Unlike some other *Diptera* which might be used in a study of predaceous and parasitoid behavior, adults of most *Sciomyzidae* are fairly large and are so distinctive that they can be readily identified while still alive in the collecting net. Also, the immature stages and the adults are rather hardy and not overly active; they can be transported easily and maintained in simple rearing chambers in the laboratory for long periods. The fact that large numbers of many species can be reared rather easily and quickly should aid in the investigation of problems which can be best approached by quantitative, experimental studies in the laboratory.

As extensive data from behavioral, ecological, taxonomic, and other approaches are integrated within a phylogenetic-systematic framework, a rather complete understanding of the evolution of this intrinsically interesting group of animals should develop. Following the outstanding taxonomic revision of the genus by J. VERBEKE, the present study of the biology of *Knutsonia* hopefully may contribute toward that objective.

TAXONOMIC CHARACTERS AND RELATIONSHIPS OF THE GENUS

The generic name *Knutsonia* was proposed by VERBEKE (1964) for *Elgiva albiseta* (SCOPOLI) 1763 and its congeners when it was discovered that *Elgiva* should be restricted to *Musca cucularia* LINNÉ and related species, and that there was no available generic name in synonymy. The synonymies are summarized below (1) :

Knutsonia VERBEKE, 1964 : 3 (type species : *Musca albiseta* SCOPOLI, 1763 : 341)
Chione ROBINEAU-DESVOIDY, 1830 : 679 (preoccupied by *Chione* MEGERLE, 1811, *Mollusca)*
nec Ilione HALIDAY, 1837 : 288
Elgiva Auct., nec RONDANI, 1858.

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(1) Recently, COLLIN (Ent. Rec. and Jour. Variation, 78 : 227-230, 1966) questioned the validity of the generic name *Knutsonia* VERBEKE, 1964. Subsequently, STEYSKAL (Ent. Rec. and Jour. Variation, in press) discussed the problem in detail, concurring with the conclusions of VERBEKE (1964) and the summary of synonymies presented here.

Knutsonia VERBEKE is a rather typical member of the *Tetanocerini*. The morphological features which have proved important in the generic classification of adult *Sciomyzidae* are as follows for the genus *Knutsonia* VERBEKE : 2 pairs of frontorbital bristles, ocellar bristles present, postvertical bristles divergent, no propleural bristle, vallar bristles present, all pleura with hairs, presutural bristle present, 2 pairs of dorsocentral bristles, 1 pair of prescutellar acrostical bristles, 2 pairs of scutellar bristles, dorsal surface of hind coxae with hairs, 1 pre-apical bristle on front and hind tibia, arista pubescent to plumose and entirely white to black with white base, second antennal segment as long as or almost as long as third, lunule covered or barely exposed, midfrontal stripe well-developed, fourth vein with 1 or more spots beyond ta, tp S-curved, anal vein extending to margin, anal cell truncate, 2 spermathecae, and 1 pair of surstyli. The male genitalia of all known species were described and figured by VERBEKE (1964).

As VERBEKE (1964) has pointed out, the most closely related genus appears to be the monobasic, boreal American genus *Hedria* STEYSKAL. Characters of the antennae, wings, male genitalia, and cerci especially indicate this relationship. However, *Hedria* STEYSKAL has the following features distinct from *Knutsonia* VERBEKE : ocellar and vallar bristles absent, pleura with only a few fine hairs, hind coxae bare on dorsal surface, no presutural bristle, 1 pair of dorsocentral bristles, no prescutellar acrostical bristles, 1 pair of scutellar bristles, and no spots on the fourth vein.

Prior to VERBEKE's 1964 revision, the genus *Knutsonia* had not been given thorough taxonomic study since HENDEL's revision (1903). Subsequent taxonomists, relying solely on external morphological features, were in almost complete disagreement as to the application of the 14 specific names which had been proposed by 12 authors between 1763 and 1953. VERBEKE reduced that chaotic state to seven species, and he described one new species. In addition to documenting his classification by studies of the male and female postabdomen as well as the classical characters, VERBEKE described features (especially those of the arista) which can be used to identify living adults in the field.

GEOGRAPHICAL DISTRIBUTION

The genus appears to be restricted to the western and southern parts of the Paleartic Region (Figs. 51, 52). One species *K. albisera* (SCOPOLI), is broadly distributed throughout most of Europe. *Knutsonia lineata* (FALLEN) is fairly wide ranging in central and northern Europe, and *K. rossica* (MAYER) has a very limited distribution in northwestern U.S.S.R. *Knutsonia turcestanica* (HENDEL) extends narrowly across most of the southern part of the Region. The remaining species have limited but quite distinctive ranges in the southwestern Palearctic. As VERBEKE (1964) pointed out, the western Mediterranean *K. trifaria* (LOEW) appears to be replaced in the eastern Mediterranean by a closely related, allopatric species, *K. turcestanica* (HENDEL). Another pair of closely related species may be recognized in *K. unipunctata* (MACQUART) (western Mediterranean) and *K. truquii* (RONDANI) (Damascus, eastern Meditteranean). The latter, although apparently sister-species, are not as closely similar morphologically as are *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL).

The distribution maps are based on collections we have examined (Zoological Museum at Helsinki, Zoological Museum at Copenhagen, British Museum (N. H.) at London, and the Spanish Institute of Entomology at Madrid); data provided by R. DAHL, W. HACKMAN, and K. G. V. SMITH; localities given by VERBEKE (1964); and our own collecting. In addition, records of *K. albiseta* and *K.* lineata from the following publications have been used : ARDÖ, 1957; DAHL, 1965; HALIDAY, 1833; KARL, 1935; REMM, 1959; ROZKOŠNÝ, 1959, 1963, 1965; SIEBKE, 1877; STACKELBERG, 1958 VAN DER WULP and DE MEIJERE, 1898; and publications cited by VERBEKE, 1964.

BIOLOGY

General Features of the Genus *Knutsonia* VERBEKE

Behaviorally, the genus *Knutsonia* seems to be on the main line of evolution within the *Tetanocerini* (= *Tetanocerinae*). Despite some distinct phenological differences, and possibly a considerable difference in feeding behavior of one species [*K. lineata* (FALLÉN)], the members can be characterized as typical tetanocerine predators of aquatic, pulmonate snails. *Knutsonia albiseta* (SCOPOLI) and *K. lineata* (FALLÉN), although representatives of different subgenera, are cold-adapted species and share some distinctive seasonal features. *Knutsonia corcyrensis* VERBEKE may also belong to this ecological group. The remaining reared species *(K. trifaria* (LOEW), *K. turcestanica* (HENDEL), and *K. unipunctata* (MACQUART)) are behaviorally similar, warm-adapted species of the same subgenus as *K. albiseta* (SCOPOLI) and *K. corcyrensis* VERBEKE.

The habitats, permanent and temporary aquatic situations, also are typical of many tetanocerine genera (*Tetanocera, Elgiva, Sepedon, etc.*). Whereas breeding of the southern species probably is continuous and leads to as many as eight generations per year, species distributed in central and northern Europe may be restricted to one generation each year. These univoltive species do not oviposit until a month or two after emergence during late spring, and the eggs seem to undergo a short period of diapause during late summer and early fall. Larval development apparently takes place during late fall, is interrupted by low winter temperatures, and is resumed and completed during early spring. The subsequent pupal period is rather short.

Emerging throughout the year in warmer areas, the southern species readily mate and begin ovipositing. The egg production, reaching an observed maximum of 461, is typical of *Tetanocerini*. Eggs hatch after an incubation period of about one week, and the larvae begin preying on snails at the surface film. As many as 40 snails, ranging from 0.8 to 8.0 mm in diameter, are eaten during the 21 to 77 days required for development through all three stadia. Whereas larvae of *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL) are overt predators of non-operculate snails and consume the entire soft parts of each victim, larvae of *K. unipunctata* (MACQUART) show a strong predeliction for certain operculate snails and characteristically eat only a portion of the soft parts. Lobing of the posterior spiracular discs also indicates that larvae of *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL) frequent more open water than do the larvae of *K. unipunctata* (MACQUART). The pupal period requires 13 to 25 days. Puparia, like those of the cold-adapted species, are formed in the water and are strongly adapted for flotation. The details of the life cycles are presented in the following sections and are summarized in Table 2.

Knutsonia albiseta (SCOPOLI), 1763

Entomologia Carniolica. 341.

Knutsonia albiseta (Fig. 3) is the most common and most wide ranging species in the genus. Its known distribution extends from Scotland (Caithness) and the lower latitudes of Fenno-Scandinavia southward throughout Europe to the northern coast of Africa and east to Turkey (Fig. 51). We have reared a few individuals from the egg to adult stage. The basic outline of the life cycle can be gleaned from this combined with other significant laboratory and field information. However, several features, especially seasonal aspects and microhabitat requirements of the first-instar larvae, make the species difficult to work with. Further study of the autecology of *K. albiseta* (SCOPOLI) is required.

Numerous adults and purparia have been found by us at a variety of aquatic habitats in Sweden, Denmark, England, Belgium, France, Austria, Italy, and Greece (1959, '60, '63, '64), but we have found only one larva in nature. This individual was found floating among emergent vegetation in a marsh in Corfu, Greece during April. Both puparia and larvae have obvious morphological adaptations for an aquatic existance. However, *K. albiseta* (SCOPOLI) is not restricted to permanent aquatic situations. In fact, the largest collection of puparia of this species (414 individuals) was made at a vernal pond (Lago San Antonio, Latina, Italy). In addition to the above records, we have found puparia floating in small, weed-choked irrigation ditches between garden plots and in a permanent pond in Corfu during April. As explained in more detail below, *K. albiseta* (SCOPOLI) is able to exploit temporary as well as permanent aquatic situations, probably because it has only one brood per year and the larvae develop only during the cooler, wetter months. When revisited in September, 1964, the

« ponds » at Lago San Antonio were dry, dusty depressions. In that Mediterranean climate, they routinely become dry by late spring and remain dry throughout the summer and early autumn.

Adults collected in Greece, Belgium, and England during spring and early summer and adults which emerged from puparia collected during spring in Italy lived a long time in the laboratory but showed a very low level of sexual activity and produced no or relatively few eggs. Four females and one male collected in Corfu, Greece between April 29 and May 8 lived 23 to 41 days, did not mate, and the females did not oviposit. Two females and one male taken in Hertfordshire, England on June 15 lived 33 to 88 days, were not seen mating, and the females did not oviposit. Three females and two males collected July 4 in Flandre orientale, Belgium lived 60 to 126 days in captivity, but mating was seen on only one occasion (August 28). Only 111 eggs were produced between July 20 and October 22, each female laying from 16 to 60 eggs. Nineteen females and 12 males which emerged between April 20 and 28 from puparia collected between April 6 and 11 at Lago San Antonio, Latina, Italy lived 15 to 187 days, were not seen to mate, and only a few eggs (unfertilized) were laid. Fifty-six females and 70 males emerged from 157 puparia that had been collected at Lago San Antonio on the same date as the individuals mentioned above and sent to Q. C. CHOCK (then State Entomologist of Hawaii). CHOCK (*in litt.*) reported that the adults lived from April 20 to August 5. Only one pair copulated, and that evidently was induced by shock treatment. A pair of adults held overnight at 7 C and exposed to direct sunlight the next morning mated 15 minutes later. None of the adults that emerged in Hawaii oviposited.

On the other hand, adults collected during the late summer in Denmark mated frequently and produced large numbers of fertile eggs. One of two females collected August 10 in Zealand, Denmark and kept in a breeding jar without a male laid 83 viable eggs between August 13 and September 5, the day she died. The other female was kept with a male. This pair mated repeatedly between August 23 and September 9; that is, until several days before the male died. The female laid 375 eggs (most of them fertilized between September 22 and November 21. We know of only one record of adults collected *in copula* : October 17, 1960 at Scarning, Norfolk, England (K.C. DURRANT, *in litt.*).

No pre-copulatory behavior was observed, and the mating posture itself was quite similar to that of other species in the genus. While mating, the male placed his front tarsi on the parafrontal area of the female's head; the apices of this middle tibiae rested on the costal margins of her partially extended wings; and the apices of the male's tibiae and the first tarsal segments grasped her postabdomen ventrolaterally.

Eggs were laid singly or in groups of two to six in no discernable pattern on grass included in breeding jars or on the walls of the glass jars. They were firmly cemented in place. Eggs were not laid on living or dead terrestrial and aquatic snails.

Our preliminary investigations indicate that the principal hatching stimulus may be much like that which operates in the hatching of the eggs of floodwater mosquitoes. Eggs laid between July 20 and October 22 by females collected July 4 in Belgium were kept on moist filter paper, and the percent which hatched was very low. Incubation periods of 33 to 76 days at room temperature were required, although the eggs appeared well embryonated as early as 21 days before hatching. Some eggs dissected on the 25th to 47th day of incubation contained living larvae. In fact, one of the larvae reared to pupation was obtained by dissecting it from the egg membranes. Quite different incubation periods were obtained from eggs laid between August 13 and November 21 by females collected on August 10 in Denmark. Some of these eggs were left in place on dry grass or on the walls of the jars, and others were transferred to moist filter paper within one week after being laid. A few eggs hatched while on these substrates, the incubation period ranging from 20 to 24 days. The remaining eggs then were completely submerged in tap water. A large proportion (about 30 %) of each group of eggs hatched within 24 hours after they were submerged. The shortest incubation period noted was 14 days, although some eggs submerged within seven days after they were laid required up to 45 days to hatch.

Like most other fresh-water insect larvae, the aquatic sciomyzid larvae reared before the present study are primarily air-breathers throughout their development. Three species of *Renocera* and *Hedria mixta* STEYSKAL in North America (FOOTE, *in litt.*), and *Knutsonia albiseta* (SCOPOLI), and *K. lineata* (FALLÉN) are the only sciomyzid larvae known to spend long periods of larval life completely submerged, evidently utilizing dissolved oxygen for respiration. Larvae of *K. albiseta* (SCOPOLI) which hatched from eggs kept on wet paper appeared flaccid and moved about listlessly. On the other hand, many larvae which hatched from submerged eggs continued to live totally submerged for 8 to 11 days in an open vial of tap water (2 × 5 cm). These larvae wriggled about actively on and near the bottom of the vial; none were seen near the surface. Although species of aquatic snails were kept in the vial with the submerged larvae, none of the larvae attacked any of these snails.

Only two larvae were reared from hatching to pupation, and only one of the two reared puparia produced an adult fly. It seems likely that failure to reproduce the proper microhabitat conditions, rather than failure to find suitable hosts, was responsible for our poor results in rearing the species in the laboratory. Plastic boxes with substrates of wet filter paper or small jars containing wet sand were used during the earlier attempts to rear larvae. Thereafter, larvae were kept in vials of tap-water.

An egg laid during the first week of October, 1959 was dissected on November 7 and the living larva was removed. The larva began to feed immediately when it was placed on a small, crushed *Physa*. This larva ate crushed *Helisoma trivolvis* (SAY), *Lymnaea palustris* (MÜLLER), and

Physa sp. during the first four days of development, and killed snails of these species during the rest of its life. The total duration of the larval stadia of this individual was 35 days (first stadium, 10 days; second, 5 days and third, 20 days). The larva did not eat during the eight days prior to puparium formation.

Four living larvae were dissected on November 14, 15, and 20, and December 5 from eggs laid between September 5 and October 20, 1959. These larvae immediately ate crushed *H. trivolvis* (SAY), but they died during the first stadium.

One larva hatched on October 15 from an egg laid between September 5 and 10. The larva fed on crushed *H. trivolvis* (SAY), *L. palustris* (MÜLLER), and *Physa* sp. for 16 days, after which time it killed and ate snails of the same three species. The total duration of larval life was 34 days. The first stadium lasted 10 days; the second, 8 days; and the third, 16 days. The larva did not eat during the seven days prior to puparium formation.

Second- and third-instar larvae of *K. albiseta* (SCOPOLI) behaved in several ways as typical predators. They killed the prey rather quickly, fed in the fresh tissues for only a few hours, and then attacked another living snail when they became hungry again. They showed definite preference for fresh tissues, and none of the larvae ate decayed snails. If the first-instar larvae normally live beneath the surface film, the feeding habits may be somewhat different from those described above for second- and third-instar larvae. Larvae were found resting most commonly between the wet filter-paper and the box, or buried up to the posterior spiracular disc in wet sand. They were observed frequently to swallow air until a large bubble collected in the gut.

Two reared adults in the British Museum (N. H.) which are pinned with puparia bear labels giving some detailed information. A larvae was collected at Golding's Wood, Hertfordshire, on March 15, 1950, by E. S. BURROW, and was reared by R. L. COE. The larva pupated April 20; the adult female emerged June 1. The other larva was collected at Cambridge on June 10, 1910 by F. EDWARDS. The reared adult is labelled, « larva elongate, green, feeding on weeds at surface of water of small pond. F. W. E. ». The larva of *K. albiseta* (SCOPOLI) is elongate but not green. The larva of *Elgiva rufa* PANZER also is elongate and the fat bodies, but not the gut, are bright green. It is the only green sciomyzid larva that we know that occurs in Europe, and larvae have been found during early June at about the same latitude as Cambridge (near Brussels, Belgium; KNUTSON and BERG, 1964). EDWARDS' notation that the larva was found feeding on aquatic vegetation may have been prompted by his confusing the green fat bodies with the gut, and undoubtedly is incorrect. A few earlier workers also have reported foods other than mollusks for some sciomyzids, but none of these claims has been verified during our rearing of over 160 species.

The two larvae which we reared in the laboratory formed their puparia on wet sand. One puparium was formed on November 18, 1959, and the male adult emerged 12 days later. The other puparium was formed on December 11, 1959. On January 23, 1960, it was taken from the heated laboratory (22 C) and placed at 5 C. It was returned to room temperature on March 29 and held for two months but no adult emerged.

Puparia have been found in nature only during spring, and adults emerged shortly after collection. Puparia were collected by us for the first time on March 30, at Lago San Antonio, when 98 individuals were taken during a search lasting one hour. All puparia were floating in the vernal pond and they were seen readily among the sparse vegetation. No larvae or empty puparia were discovered, thus indicating that all members of the population were at approximately the same stage of development. Some puparia evidently were recently formed. These were unpigmented; they contained pre-pupae, not pupae; and pulsations of the tracheal trunks could be seen through the integument. All 98 puparia were taken to a heated laboratory and 98 adults emerged between April 1 and 15. On April 6 and 11, 314 puparia were collected at Lago San Antonio. They were placed in a refrigerator for a few days; then half were sent to Ithaca, N. Y. and half to Hawaii. From these puparia, 256 adults (114 females, 142 males) emerged between April 20 and 30 (CHOCK, *in litt.)*. A fourth visit to Lago San Antonio was made on May 6. Only two intact puparia were collected, both of which produced adults about May 11. Surprisingly few empty puparia were found; these may fill with water and sink. A female emerged April 27 and a male emerged April 29 from two puparia collected April 23 in Corfu, Greece. Thus, from a total of 416 puparia collected between March 30 and May 6, 358 adults emerged between April 1 and May 11.

An adult pinned with its puparium in the Natural History Museum, Vienna, is labelled, « Puppe im Sumpfwasser, schwimmend gefunden. Parndorf. Mai, 1874. » An adult pinned with its puparium in the Zoological Museum, Copenhagen bears a label stating that the puparium was collected June 27, 1911 and the adult emerged July 14. The latter record may support Edwards' report of finding a larva on June 10 in England. The record also indicates that in northern Europe the beginning of the flight period is quite variable and some individuals may emerge much later than one would suppose from inspection of date-locality records.

Adults which emerged in the laboratory lived 15 to 187 days; those collected in the field lived 23 to 126 days after capture. Males and females were about equally long-lived. Adults collected during spring lived longer than those captured during autumn.

In his interesting study of the possibility of utilizing museum specimens in ethological and ecological investigations, Soós (1958) used the *Sciomyzidae* as test animals. He placed *K. albiseta* (SCOPOLI) in his group three, « Nicht eurychrone Arten », and gave the flight period as May 6 to October 20 in the Carpathian Basin. Other capture dates of adults are as follows, Scotland : June 17 to August 27 (British Museum); England, Wales and Ireland : May 1 to September 30 (British Museum); southern Finland : June 14 to August 5 (HACKMAN, *in litt.*); Denmark : June 12 to October 8 (KNUTSON and LYNEBORG, 1965); southern Sweden : June to September (WAHLGREN, 1917); Estonia : June 25 to September 2 (REMM, 1959); Belgium : May to September (VERBEKE, 1948); and Czechoslovakia : May 17 to November 15 (ROZKOŠNÝ, 1963). In addition, we have taken adults in Latina, Italy and Corfu, Greece, between March 24 and May 8.

On the basis of interruptions in the seasonal distribution of 94 date-locality records, Soós (1958) speculated that *K. albiseta* (SCOPOLI) has at least three generations per year. Our laboratory and field observations indicate strongly that only one generation is produced each year and that overwintering takes place in the larval stage.

The fact that no parasitoid *Hymenoptera* have been reared from the many puparia found during spring tends to confirm other indications that the larvae are active during only the cooler months (when the wasps apparently are not active) and that overwintering occurs in the larval stages.

Knutsonia corcyrensis VERBEKE, 1964

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Knutsonia corcyrensis was described from a large series of specimens collected by the senior author on the Greek island of Corfu, and is known only from the type material (Fig. 51). The species occurs with, and is superficially very similar to *K. albiseta* (SCOPOLI), but it is distinct from the latter on characters of the arista, fourth sternite of the male abdomen, male genitalia, and female spermathecae (VERBEKE, 1964). Adults and puparia were collected but a laboratory rearing was not obtained.

All of the localities where *K. corcyrensis* VERBEKE has been collected seem to be permanent-water situations and are exposed to direct sunlight. They support moderate to dense populations of *Physa* sp., *Planorbis* planorbis (LINNÉ), *Lymnaea palustris* (MÜLLER) and *Succinea* sp.

Puparia were most numerous in a fresh-water marsh just west of Lake Antinioti, a large lake situated at the northern end of the island, 43 km north of the city of Corfu. The extensive, rather deep, marshlike margin supports a dense growth of *Phragmites* and other aquatic vegetation, and large aquatic leeches as well as aquatic snails are extremely numerous. Puparia were found floating among aquatic vegetation. Thirteen puparia were collected on April 23, and 11 were found on May 8. Other sciomyzids present as adults were : *Elgiva cucularia* (LINNÉ), *Knutsonia albiseta* (SCOPOLI), *Sepedon s. spinipes* SCOPOLI, and *Tetanocera ferruginea* FALLÉN.

Small, slowly flowing, and week-choked irrigation ditches between garden plots at Hricida, 7 km southwest of Corfu, produced the second largest number of puparia (two, April 27; four, May 1; two, May 4; one, May 7; and two, May 12). Other adults collected here were : *Elgiva cucularia* (LINNÉ) *Pherbellia ventralis* (FALLÉN), *Pherbina coryleti* (SCOPOLI), *Psacadina punctata* (FABRICIUS), *Sepedon s. spinipes* (SCOPOLI) *Tetanocera arrogans* (MEIGEN), and *T. ferruginea* FALLÉN.

Four puparia were found floating in a grass-sedge marsh at Gardiki, 22 km south of Corfu (and 37.8 airline-kilometers south of Lake Antinioti, the northern most collecting site) on April 29. Adults of *K. albiseta* (SCOPOLI) *Pherbina coryleti*, (SCOPOLI), *Psacadina punctata* (FABRICIUS) *Sepedon s. spinipes* (SCOPOLI), *Tetanocera arrogans* (MEIGEN), and *T. ferruginea* (FALLÉN) also were found at the marsh.

One puparium was taken among emergent vegetation in an irrigation ditch at Ropa, 12 km south of Corfu, on April 26. Adults of *K. albiseta* (SCOPOLI) and *Tetanocera ferruginea* FALLÉN also were found at Ropa.

One puparium was found in a shallow *Phragmites* marsh at Merlin, near Tzavrou, 9.5 km north of Corfu, on May 9. Adults of *Hydromya dorsalis* (FABRICIUS), *Knutsonia albiseta* (SCOPOLI), *Pherbellia grisescens* (MEIGEN), *P. ventralis* (FALLÉN), *Pherbina coryleti* (SCOPOLI) *Psacadina punctata* (FABRICIUS), and *Tetanocera ferruginea* FALLÉN were found at Merlin.

From the total of 43 puparia found between April 23 and May 12, 1963, adults emerged 1 to 16 days after the puparia had been collected. Forty-three adults emerged between May 4 and 24 (21 males, May 6 to 24; 22 females, May 4 to 23). No parasitoid Hymenoptera were obtained from the field-collected puparia.

Nine pairs of adults which emerged in the laboratory were placed in breeding jars. The results, which were similar to those noted in studies of *K. albiseta* (SCOPOLI), indicate that *K. corcyrensis* VERBEKE is univoltine also. Copulation was not seen, none of the females appeared to be gravid, and no eggs were laid. The adults lived 2 to 72 days after emergence (males, 6 to 40 days, average = 27.5; females, 2 to 72 days, average = 23.7).

Knutsonia trifaria (LOEW), 1847

Stettiner entomologische Zeitung. 8 : 246.

Although evidently closely related to *K. turcestanica* (HENDEL), *K. trifaria* (LOEW) may be distinguished by its mainly white arista and by the spermathecae, male genitalia, and color pattern of the thorax as given by VERBEKE (1964).

The known distribution extends from Spain (La Coruña) and Morocco (Asni, Atlas Mts.) eastward to Dalmatian Yugoslavia (Salona) and Sicily (Syracuse) (Fig. 52). The northern-most record is Landeck, Tirol, Austria.

We have found the species at several rather different habitats in southern Spain during 1964. Adults and puparia were collected most abundantly between January 29 and March 13 at the margins of small ponds, drainage ditches, and in flooded, disused agricultural plots at the Albufera de Adra, an intensively cultivated, spring-fed marshy region along the coast west of Almeria. The area supports a rich growth of herbaceous vegetation (*Phragmites, Typha, Juncus, Lactuca,* and *Cynodon)*. Gastropods present are *Lymnaea peregra* (MÜLLER), *Planorbis planorbis* (LINNÉ), *Physa acuta* (DRAPARNAUD), *Hydrobia* sp., *Succinea elegans* RISSO, *S. pfeifferi* ROSSMÄSSLER, *S. putris* (LINNÉ), and *Agriolimax* sp. Other *Sciomyzidae* found with *Knutsonia trifaria* (LOEW) were *Pherbellia dorsata* (ZETTERSTEDT), *P. griescens (MEIGEN)*, *Hydromya dorsalis* (ROBINEAU-DESVOIDY), *Pherbina coryleti* (SCOPOLI), *Psacadina punctata* (FABRICIUS), *Sepedon h. hispanica* LOEW, *S. sphegea* (FABRICIUS), *S. s. spinipes* (SCOPOLI), *Tetanocera arrogans* (MEIGEN), and *T. ferruginea* FALLÉN. On February 28, four adults of *K. trifaria* (LOEW) and one of *Hydromya dorsalis* (FABRICIUS) were swept from herbaceous vegetation bordering a very narrow, shallow, and swiftly flowing irrigation ditch at the exposed edge of an orange grove at Rioja, Provincia Almeria. A few adults of *K. trifaria* (LOEW) were taken on March 13 among grasses and *Juncus* at the marshy margin of a large spring (Fuente de Cela) in Tijola, Provincia Almeria (Fig. 1). The senior author and J. VERBEKE collected adults along two streams, Rio Jucar at Cotes (Valencia) and Rio Palancia at Navajas (Castellón), on April 6.

Laboratory rearings were started with adults and pupae collected at the Albufera de Adra between January 29 and March 13. Adults collected between January 29 and February 26 mated between January 30 and March 14; those which emerged in the laboratory copulated within three days after emergence.

Four females collected between January 29 and February 28 oviposited between February 3 and March 29, laying 88, 172, 250, and 293 eggs. Five females which emerged in the laboratory laid 14, 58, 123, 186, and 340 eggs between February 28 and June 11. The preoviposition periods for laboratory-reared females ranged from five to ten days. Eggs were laid most commonly on pieces of fresh leaves of *Typha* and on sides of the jars; none were laid on living snails. They were placed side by side and touching each other, in groups of 3 to 18 along the margins of the leaves. The incubation period was three to seven days (usually five days) at room temperatures.

During laboratory rearings larvae of all three instars killed and ate *Lymnaea peregra* (MÜLLER), *Physa acuta* (DRAPARNAUD). *Planorbis planorbis* (LINNÉ), and *Helisoma trivolvis* (SAY). All larvae showed a strong predilection for aquatic, pulmonate snails. Third-instar larvae killed and ate *Succinea* spp., and the operculate snails *Hydrobia* sp. and *Melanopsis algerica* (PILSBRY) if the latter were removed from the water.

Larvae and living snails of various sizes were placed in rearing boxes containing water to a depth of a few millimeters or wet cotton. Larvae of all instars killed and ate snails in much the same manner. Active slashing and hooking movements of the mouthhooks were evident as soon as contact was made with a living snail. The prey at once retracted into its shell and the larva vigorously pursued it. The snail's hemocoel was ruptured within a few minutes after the initial contact, and it died shortly thereafter. The larva remained in the shell for an hour or two and rapidly consumed snail tissue until its gut was filled. Then it rested outside the shell, and when it became hungry again it killed another snail. None of the larvae fed on dead or decaying snails.

The numbers and dimensions of snails killed and eaten during the three stadia by ten larvae reared in separate containers are given in Table I. Each of these rearing dishes contained a surplus of *Planorbis planorbis* (LINNÉ), ranging from 0.8 to 8.0 mm in greatest diameter. The total duration of larval life ranged from 22 to 30 days. The first stadium was 6 to 8 days; the second, 6 to 9 days; and the third, 9 to 15 days.

The ability of third-instar larvae to prey successfully on an operculate snail such as *M. algerica* (PILSBRY) (which has a rigid, calcareous operculum) is an unusual feature of *K. trifaria* (LOEW). Most sciomyzid larvae which have been placed with operculate snails during feeding trials were killed when they were caught between the shell and operculum of the retracting snails (NEFF, 1964). The larvae of *K. trifaria* (LOEW) ate all of the soft parts of operculate snails except the muscular tissue attached to the operculum (Fig. 2B).

Fifty-nine larvae formed puparia between March 1 and 18. All were formed in the water or on wet cotton, not on drier surfaces such as the lids of the rearing containers. Eighteen males and eighteen females emerged from these puparia between March 18 and April 3, after pupal periods of 14 to 18 days (average, 15.1 days). Eight puparia found floating among emergent grasses on February 19 produced adults (five females, three males) between February 23 and March 5.

Comparable longevity records for adults reared in the laboratory and for adults collected in the field indicate that the laboratory diets provided larvae and adults were adequate. Fifteen field-collected adults lived 17 to 96 days (average, 37.8 days) in captivity. Eight adults which emerged from field-collected puparia lived 14 to 109 days (average, 36.0 days). Eight laboratory-reared adults lived 17 to 85 days (average, 50.7 days).

Although there are no field data for the summer and autumn months, laboratory observations indicate that the species breeds continuously throughout the year in the warm climates that prevail throughout most of its range. Breeding probably ceases during the cooler months in the northern parts of the range.

Adults have been collected during all months between January 29 (Adra, Spain) and October 20 (Amelie-les-Bains, Pyrenees Orientales) in the warmer parts of the range, and as late as August 15 (Landeck, Austrian Tyrol) at the northern limit of known distribution (VERBEKE, 1964).

With a preoviposition period of 5 to 10 days, an incubation period of 3 to 7 days, a larval life of 22 to 30 days, and a pupal period of 14 to 18 days, the entire life cycle must require 44 to 65 days. It seems likely that five to eight generations may be produced during one year of continuous development.

Knutsonia turcestanica (HENDEL), 1903

Zeitschrift für Hymenopterologie und Dipterologie. 3 : 214.

Knutsonia turcestanica (HENDEL) has been characterized by VERBEKE (1964) as a geographical vicariant, or replacement species, of *K. trifaria* (LOEW) from the western Mediterranean region. The species is known to range from Serbian Jugoslovia (Niz) across the eastern Mediterranean and southwestern Asia to Turkestan (Djarkent) (Fig. 52). The behavior and morphology of the immature stages, as well as the adult morphology which has been studied by VERBEKE (1964), show that *K. turcestanica* (HENDEL) and *K. trifaria* (LOEW) are closely related species. *Knutsonia turcestanica* has a mainly black arista, whereas that of *K. trifaria* (LOEW) is mostly white; the antennae, spermathecae, and male genitalia were figured by VERBEKE (1964).

We have collected *K. turcestanica* (HENDEL) at two places on Crete and at one locality in Afghanistan. Adults were found most abundantly between March 21 and April 12, 1963 at a small, spring-fed, exposed marsh on the northern coast of Crete at Gerani, 15 km west of Canea. Large groups of *Juncus*, a low, emergent species of *Ranunculus*, and hygrophilous grasses formed the dominant vegetation. Much of the marsh had only a few centimeters of water, but there were small pools and channels throughout the area. Other *Sciomyzidae* found there were *Hydromya dorsalis* (FABRICIUS), *Psacadina punctata* (FABRICIUS), and *Sepedon s. spinipes* (SCOPOLI). The only aquatic and hygrophilous gastropods found at Gerani were *Lymnaea peregra* (MÜLLER), *Planorbis planorbis* (LINNÉ), and *Succinea* sp. A few adult flies were swept from emergent vegetation at the marshy margin of a spring-fed lake, Agia, nine km southwest of Canea on April 13, 1963, and a few were found by sweeping over a small brook at Ghazni, Afghanistan on October 6, 1964.

Laboratory rearings and observations were started with adults collected between March 21 and April 12, 1963 at Gerani, Crete. Adults collected on March 21 copulated the following day, and continued to mate at intervals until April 24. Mating can occur in nature before April 1; a female collected on that date and kept from males in the laboratory subsequently laid viable eggs.

Four females collected in nature oviposited between March 23 and June 4 in the laboratory, laying 157, 173, 176, and 211 eggs. A female which emerged in the laboratory on May 21 was seen to mate for the first time on May 28, and laid her first egg on May 29. Eggs were laid on pieces of fresh *Typha* leaves and on the sides of the jars. They were placed side by side and touching each other, in vertical rows of 2 to 41, along the edges of the leaves. The incubation period was six to eight days at room temperatures.

Larvae killed and ate mature individuals of *Planorbis planorbis* (LINNÉ), *Physa acuta* (DRAPARNAUD), and *Lymnaea peregra* (MÜLLER). They fed on the embryos in punctured egg capsules of *L. peregra* (MÜLLER), but did not penetrate entire egg capsules of *L. peregra* (MÜLLER) or *P. planorbis* (LINNÉ). Third-instar larvae ate crushed individuals of *Viviparus* sp., but starved when placed in rearing dishes of living, mature individuals of these operculate snails.

Larvae were kept in rearing dishes containing water to a depth of a few millimeters and several species of aquatic, pulmonate snails. Larvae of all instars fed in an overtly predaceous manner very similar to that of larvae of *K. trifaria* (LOEW). The prey were vigorously pursued and quickly killed. The larvae fed on fresh tissues until only their immediate hunger was satisfied, rested outside the shells when not feeding, and killed and ate a large series of snails during development through the three stadia. The total duration of larval life ranged from 32 to 39 days. The first stadium was 9 to 11 days; the second, 7 to 9 days; the third, 16 to 19 days.

All larvae formed their puparia in water or on wet cotton. Thirty-six larvae pupated in the laboratory between May 2 and 22. Sixteen adults (ten females, six males) emerged between May 17 and 28 after pupal periods of 13 to 15 days. Puparia which did not produce adults were dissected and found to contain dead pupae.

Adults collected between March 21 and April 12 lived 44 to 116 days (average, 56.0 days) in capacity. Each of two adults which emerged in the laboratory lived 20 days.

The only dates of collection of adults available are March 21 to April 13 in western Crete; April 16 at Mugla, southwestern Turkey; May, at Quetta, Pakistan (VERBEKE, 1964); and October 6, 1964 at Ghazni, Afghanistan. If breeding is continuous throughout the year, it seems likely that five or six generations are produced.

Knutsonia unipunctata (MACQUART), 1849

in H. Lucas, Exploration Scientifique de l'Algérie. Zool. III, Diptères : 494

Knutsonia unipunctata (MACQUART) has had a very confused taxonomic history, as VERBEKE (1964) has shown. Various European taxonomists have referred to *K. unipunctata* (MACQUART) under four synonyms in addition to the valid name. The species seems to have an eastern Mediterranean vicariant in the rarely collected *K. truquii* (RONDANI), and may be separated from it by the following combination of characters : second antennal segment not inflated, mid-frontal stripe broad and convex, inferior costal spines elongate on second and third sections, and posterior surface of hind coxae with fine setae.

The known distribution of *K. unipunctata* (MACQUART) (Fig. 52) is restricted to the western Mediterranean, where it ranges from Spain (Madrid) and Morocco (Tangier) eastward to Sardina, and France (Sospel) (VERBEKE, 1964).

Immature stages have not been found in nature. We have collected adults at only one locality, Fuente de Cela (Fig. 1), a large spring at Tijola, Provincia Almeria, Spain (February 21 and March 12, 1964). The spring-pool is used frequently as a place for washing clothes and thus much of it has been modified from the natural condition. One side is almost devoid of vegetation, a concrete access-platform crosses one end, and concrete channels carry off most of the water. However, the pool is bordered on one side by a small marshy area through which several small streams flow. *Juncus* forms the dominant herbaceous vegetation and the area is partially shaded by small trees and *Nerium* sp. An operculate snail, *Melanopsis algerica* (PILSBRY), is very abundant in the pool, and *Succinea* sp., *Lymnaea peregra* (MÜLLER), and *Physa acuta* (DRAPARNAUD) are fairly common in the marshy area. Other *Sciomyzidae* taken at this locality were : *Pherbellia cinerella* (FALLÉN), *P. dorsata* (ZETTERSTEDT), *P. griseola* (FALLÉN), *Psacadina disjecta* ENDERLEIN, *Knutsonia trifaria* (LOEW), and *Sepedon sphegea* (FABRICIUS).

Adults taken on February 21 and March 13 continued to mate at intervals from the day after they were collected until June 2. Adults which emerged in the laboratory during July mated a few days after emergence. While mating, the basicostal margins of the female's half-extended wings were gripped in the axillae of the male's femoral-tibial joints and the apices of the male's hind tibiae grasped the sides of the postabdomen while his hind tarsi hung freely.

Five females collected on February 21 and March 13 oviposited in the laboratory between February 25 and July 9, and laid 54, 55, 154, 208 and 447 eggs. A female which emerged in the laboratory on June 13 had a preoviposition period of 43 days and laid 461 eggs between July 26 and November 12. Eggs were laid commonly on pieces of fresh grass leaves, occasionally on the walls of the jars, and rarely onto the gauze covers. When laid on leaves, the eggs were placed in groups and side by side at right angles to the main veins. Unlike those of *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL), the eggs did not touch each other and their posterior apices were placed toward the center of each leaf. Eggs laid between February 25 and November 12 hatched after incubation periods of six to seven days at room temperatures.

As those of other species, larvae of *K. unipunctata* do not seem to be very host specific. They killed and ate several species of snails not occurring within their range. During laboratory rearings, larvae killed and ate living individuals of the following aquatic, pulmonate snails : *Australorbis glabratus* (SAY), *Helisoma trivolvis* (SAY), *Planorbis planorbis* (LINNÉ), *Aplexa hypnorum* (LINNÉ), *Physa acuta* (DRAPARNAUD), *Lymnaea glabra* (MÜLLER), *L. palustris* (MÜLLER), and *L. peregra* (MÜLLER). Larvae also readily killed and ate the hygrophilous snail *Phytia myosotis* (DRAPARNAUD), but they seldom attacked *Succinea* sp. and were unsuccessful in attempts to feed on *Hydrobia* sp., an operculate snail.

Although larvae developed to pupation on aquatic, pulmonate snails, they behaved quite differently from larvae of *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL). They were not as active as the latter two, seemed to prefer a damp substrate rather than water, usually did not kill the food snail immediately upon entering its shell, left large amounts of uneaten snail tissue, and required considerably longer to complete development.

First-instar larvae fed as readily on freshly crushed snails as on entire, living snails. *Planorbis planorbis* (LINNÉ) was the preferred food snail during the first stadium, but *Phytia myosotis* (DRAPARNAUD) seemed to be preferred during the third stadium. The attack and feeding behavior were similar during all three stadia. Larvae forcibly entered living snails, but did not penetrate as quickly as did larvae of *K. trifaria* (LOEW) and *K. turcestanica* (HENDEL). The *K. unipunctata* (MACQUART) larvae penetrated deeply between the mantle and shell and fed in the upper whorls of the spire, consuming the ovotestis and digestive gland (Fig. 2). They continued to feed there for several hours and then withdrew, leaving the muscular foot and mantle intact. Often, slight waves of muscular contractions were seen in the uneaten soft parts after the larva had left the shell. Larvae characteristically retired to a corner of the rearing box or crawled under the cotton or filter paper in the bottom of the box and remained there for a few days between each meal. The long durations of the larval stadia do not reflect active and continuous feeding but rather a great deal of time spent in a more or less torpid state between feeding periods of moderately short duration. The total length of larval life ranged from 46 to 75 days (first stadium, 14 to 21 days; second, 13 to 16 days; and third, 19 to 40 days).

A large number of larvae were reared in the laboratory, but most of them died during the third stadium and only eight formed puparia. Larvae pupated between April 25 and June 7, and adults (five females, two males) emerged between May 15 and June 22 after pupal periods of only 15 to 25 days.

Adults collected on February 21 and March 13 lived 9 to 53 days, except for one female taken on March 13 which lived 117 days. A female and a male which emerged in the laboratory on May 27 and April 25 lived 158 and 188 days respectively.

There are only a few dates of capture of adults, ranging from February 21 (Tijola, Spain) to July (Orihuela, Spain) (VERBEKE, 1964). If a rather long preoviposition period of about 40 days is typical of the species, there are probably only two or three generations per year, even assuming continuous breeding.

Knutsonia lineata (FALLÉN), 1820

Diptera Sueciae, Sciomyzides, 11.

According to VERBEKE (1964), *Knutsonia lineata* (FALLÉN) has been determined correctly by all European dipterists who have published information under the name. The species should not be confused with the rare *K. rossica* (MAYER), known from northwestern U. S. S. R. Other than by details of the postabdomen, *K. lineata* (FALLÉN) may be separated from *K. rossica* MAYER by the presence of strong vallar (subalar) bristles, a dark spot on the fourth vein between the crossveins, and a brown middorsal thoracic stripe in the former.

Knutsonia lineata (FALLÉN) is a relatively uncommon species distributed throughout northern and central Europe. It is known to range from Scotland (Sutherland), Finland (Kuusamo), and U. S. S. R. (Arkhangelsk Province) southward to France (Paris), and Hungary (Kecskemét) (Fig. 51). Records of « *Elgiva lineata* » from North America apparently were based on specimens of *Hedria mixta* STEYSKAL and *Elgiva rufa* PANZER (STEYSKAL, 1954, 1965).

None of our attempts to rear this species through the complete life cycle in the laboratory was successful. However, the information that was obtained is presented here because it may provide some clues that would aid in a successful rearing.

We have collected adults abundantly at only three places : Tvärminne, Hango Peninsula, southern Finland; Lake Erken, Sweden; and Suserup, near Sorø, Denmark. The Suserup locality also in the only place where any immature stage (a puparium which subsequently produced an adult) has been found. At Tvärminne, *K. lineata* (FALLÉN) was the most commonly encountered sciomyzid between July 11 and August 5, 1963 at a small, vernal marsh (Byträsket) where *Salix repens* LINNÉ, *Ledum palustre* LINNÉ, *Potentilla palustris* (LINNÉ), *Carex houghtonii* FARRE, and *C. rostrata* STOKES (det. H. LUTHER) were the characteristic plants. Adults were collected between August 3 and 8, 1959 at a marsh-like area along the shore of Lake Erken. The third locality is a small, vernal marsh surrounded by a cultivated field, a pasture, and a highway, two km north of Suserup, Denmark. *Salix, Carex, Potentilla* and *Eriophorum* are the dominant plants in this marsh, and *Anisus nitidus* (MÜLLER), the calcifuge *Lymnaea glabra* (MÜLLER), and finger-nail clams are the most common mollusks. Other *Sciomyzidae* were taken at this site between May 12 and August 25 but *K. lineata* (FALLÉN) was found only between June 22 and August 8. A few adults also were taken in a vernal swamp at Frederikslund, near Holte, Denmark.

Attempts to initiate rearings were made with 39 adults (15 males, 24 females) collected between July 11 and August 8 in Finland, Sweden, and Denmark. The adults were moderately long-lived in the laboratory. Males lived 20 to 87 days (average, 40.8 days), and females lived 15 to 137 days (average, 61.4 days). There was little sexual activity in laboratory breeding jars. Copulation was observed between July 13 and September 20, but was frequent only during the latter half of August and during September. Eggs were laid between August 2 and December 10. Sixteen females laid 1, 2, 7, 11, 20, 23, 29, 33, 36, 37, 58, 78, 100, 102, 116, and 151 eggs. A female collected on July 31, and kept isolated from males in the laboratory, laid viable eggs between September 11 and 23. Three females collected on August 8 and kept apart from males laid viable eggs between August 8 and 23, between August 16 and October 31, and between August 22 and December 10.

Eggs were placed singly or in disorganized groups and were cemented to drier substrates in the breeding jars, such as the gauze covering, shells of crushed snails, or dry pieces of grass leaves. Subsequently, eggs were removed from the breeding jars and placed on damp cotton in rearing containers. Embryonation proceeded directly, within four to seven days at room temperatures, but the eggs did not hatch in this situation. Exposure to temperatures of − 6, 0, and 5 C for periods up to 86 days, and subsequent exposures to room temperatures did not stimulate hatching. During later rearing attempts, we discovered that eggs hatch only after being totally submerged in water. Exposure to low temperatures is not required. Almost 100 % hatching was obtained when embryonated eggs were immersed completely in tap water, one to several weeks after they had been laid. Most of these eggs hatched within two to ten days after being submerged.

A few larvae were dissected from the egg shells before we discovered that immersion in water would induce hatching. All where placed on wet cotton, but they appeared flaccid, did not crawl about, and most of them died within a few days. One ate a very small amount of fresly crushed aquatic snails during the nine days that it remained alive. During subsequent rearings we learned that newly-hatched larvae did not crawl out of the water after leaving the egg membranes, but remained completely submerged. Larvae then were placed routinely in open vials containing tap water to a depth of 5 cm. The larvae remained alive and wriggling about near the bottom of vial, completely cut off from the air and without feeding for as long as 16 days. At no time were the larvae seen near the surface film. Apparently, they respire only by cutaneous diffusion of dissolved oxygen. Although the larvae never were seen in contact with the air, the internal tracheal system is very well developed. The main tracheal trunks are much longer than the larva, and lie convoluted against the body wall (Fig. 5). Also, minute tracheae and tracheoles extend into some of the elongate body tubercles and into the exceptionally long lobes of the posterior spiracular disc. There are at least three explanations for the well developed tracheal system of the first-instar larvae : (1) the convoluted tracheal trunks lying against the body wall may act as enlarged diffusion surfaces increasing the efficiency of cutaneous respiration, (2) the large tracheal trunks may serve for air storage if the larvae do in fact occasionally rise to the surface and breathe atmospheric air, and (3) the tracheal trunks may function more in maintaining a hydrostatic skeleton than in respiration.

A wide variety of living snails and eggs of snails were included with the larvae in vials of water, but none of the larvae fed on any of these gastropods. Larvae did not feed on punctured or entire egg capsules of *Lymnaea glabra* (MÜLLER), *L. palustris* (MÜLLER), *L. truncatula* (MÜLLER, or *Planorbis planorbis* (LINNÉ), or on newly hatched or mature individuals of these species or of *Anisus vortex* (LINNÉ), *Bathyomphalus contortus* (LINNÉ), *Deroceras reticulatus* (MÜLLER), *Anisus nitidus* (MÜLLER) or *Succinea* sp.

A puparium of *K. lineata* (FALLÉN) was found floating in the marsh near Suserup, Denmark on June 22, 1964. A male fly emerged on July 7.

In nature, emergence seems to be rather late in the season, and the adults apparently have only a short period of activity. The earliest record is May 3 at Rambouillet, France (VERBEKE, 1964), but most capture dates are from July and August. Adults have been taken between July 27 and August 5 in northern Finland, and between July 3 and September 1 in southern Finland and Russian Karelia (HACKMAN, *in litt.*); between June 22 and October 14 in Denmark (KNUTSON and LYNEBORG, 1965); between June 4 and August 27 in the British Isles (British Museum); and between June 20 and September 2 in Belgium (VERBEKE, 1964).

MORPHOLOGY.

Summary of Characters of the Supra-Generic Categories of the *Sciomyzidae*

Larvae of the *Sciomyzidae* can be distinguished from those of other *Diptera* by the presence of an unpaired, transverse sclerite (ventral arch) joining the anteroventral margins of the paired mouthhooks, by the absence of other sclerites in this region, by the absence of food canals around the mouth opening, and by the absence of pharyngeal ridges between the ventral cornua of the pharyngeal sclerites. Puparia also can be identified by these characters. Because the eggs of so many *Diptera* are relatively featureless and because so few are known, there is not enough information available to give a diagnostic characterization of the eggs of *Sciomyzidae*.

A discussion of the morphology of the immature stages of most subfamilial categories was presented by KNUTSON (1966). There it was shown that the characters of the larvae of the two major categories, *Sciomyzini* and *Tetanocerini* (including *Knutsonia*), are bridged by the Holarctic genera *Renocera* and *Antichaeta (Tetanocerini)*, which have some features of both tribes. Recently it has been discovered that larvae of two Neotropical genera, *Perilimnia* and *Shannonia*, have all typical characters of the *Tetanocerini* (KACZYNSKI, 1966) although adults possess the propleural bristle which has been regarded as the major diagnostic feature of the *Sciomyzini*. These facts indicate that the *Sciomyzini* and *Tetanocerini*, as presently composed, are not monophyletic groups and thus are invalid concepts for a phylogenetic-systematic study.

However, the « *Tetanocerini* » other than *Antichaeta* and *Renocera* which we and our associates have examined (*Dichetophora*, *Dictya*, *Elgiva*, *Euthycera*, *Hoplodictya*, *Hydromya*, *Limnia*, *Pherbina*, *Protodictya*, *Psacadina*, *Sepedon* and *Tetanocera*; summarized by KNUTSON, 1963) share the following features : accessory teeth present below mouthhooks, no dorsal bridge between pharyngeal sclerites, no window in dorsal cornua of pharyngeal sclerites, sinus of pharyngeal sclerite extending less than halfway to anterodorsal margin of sclerite (= indentation index less than 50), and interspiracular processes usually present on posterior spiracular plates. *Knutsonia* also has these characters and thus, on the basis of the morphology of the larvae as well as of the adults, appears to be a typical member of the *Tetanocerini*.

The Genus Knutsonia VERBEKE

Egg (Fig. 4). — Length 0.88-2.00 mm, greatest width 0.27-0.60 mm. White. Elongate-ovoid, dorsoventrally asymmetrical, ventral surface more convex than dorsal surface. Anterior end with dorsally reflected, transversely arched lip shielding micropyle dorsally; posterior end with well-developed, conical tubercle; lip and tubercle smooth, irregularly punctate. Chorion surface with densely anastomosed, finely striate, longitudinal ridges and grooves.

Larva (Fig. 5-38). — Elongate, subcylindrical, tapered and strongly retractile anteriorly, posterior end expanded. Malpighian tubules pink to brickred. Segment I distinctly divided into 2 parts : anterior part elongate, apically bilobed, each lobe bearing 2-segmented sensile papilla with darkly pigmented basal ring at apex and lightly-pigmented, ring-like sensillum ventrally; posterior part annular, with dense patch of well-developed, posteriorly directed spinules on anteroventral margin (= post-oral spinule patch). No food canals (= oral grooves) around mouth, 1 labral papilla on each side of mouth. Segment II : smooth, cylindrical, bearing pair of yellowish, elongate, anterior spiracles posterolaterally in second and third instars. III : smooth, cylindrical, ring of short, interdigitated rows of small, conical spinules around anterior margin broadest ventrally. IV : first segment bearing infuscated punctations; tubercles present but indistinct; broad ring of short, interdigitated rows of minute, conical spinules around anterior margin. II-IV : 6 transparent bristles equally spaced around segment (best seen by reflected light against black background). V-XI : similar in pigmentation, punctation, and tuberculation, but increasing gradually in size to VIII at mid-length and then tapering slightly to expanded posterior spiracular disc. Segments separated by primary integumentary folds, and each segment subdivided into 3 more or less distinct rings by 2 secondary integumentary folds which are indistinct laterally. Tubercle pattern : each anterior ring with 1 widely spaced pair ventrally; each middle ring with 2 pair dorsally, 1 pair dorsolaterally, group of 3 laterally, and 2 pair ventrally, outer pair longest; each posterior ring with 1 small, widely spaced pair ventrally. Ventral tubercles of anterior and posterior rings opposite space between inner and outer ventral tubercles of middle ring. Dorsolateral tubercle especially large and laterally displaced on XI. Dorsal tubercles of uniform size, others increasing in size posteriorly. No hair patches on tubercles; outer dorsal and upper and lower lateral tubercles each terminating in 1 long, fine bristle; dorsolaterals and inner dorsals each with 2 short bristles; ventral tubercles with dense patch of very short, moderately recurved spinules. XII narrower basally than XI, post-anal portion not an elongate « Atemrohr ». Pre-anal welt forming strongly protuberant anal proleg; antero-apical surface with several small spinules; posterior surface bare; elongate, lateral tubercle above proleg. Perianal pad (= anal plate) strongly protuberant, transverse, bilobed, bare; anus longitudinal on midline; patch of short, thick, dark spines behind pad. Four pairs of fleshy lobes around margin of posterior spiracular disc : dorsolateral lobes smallest, indistinct or hemispherical; lateral lobes short and broadly triangular or elongate; ventro-lateral and lateral lobes short and broadly triangular or elongate-lanceolate, subequal. One long, fine bristle basally and 1 subapically on ventrolateral lobe; 1 long, fine bristle anterobasally on lateral lobe. (These bristles may indicate a homology of the lobes with the lateral tubercle group and outer dorsal tubercles of the preceeding segments). One pair of posterior spiracles near center of disc in all 3 instars. Spiracular tubes rugose, on non-pigmented, dome-like swellings of central area of disc. Four well-developed, yellowish, branched, interspiracular hairs arising from openings of perispiracular gland on margin of spiracular plate.

Cephalopharyngeal skeleton length 0.322-1.200 mm; indentation index 33-52; darkly pigmented; with 6 paired or bilaterally symmetrical sclerites. Mouthhooks joined middorsally; hook-part evenly tapered to acute apex. Ventral arch transverse, strongly flexed ventrally, articulated with anteroventral margin of mouthhooks; minute, subequal, recurved teeth on anterior margin. Ligulate sclerite between and slightly below apices of anterior rami of hypostomal sclerite, strap-like, flexed anteriorly, weakly joined to plate between anterior rami. Epistomal sclerite transverse, above anterior rami of hypostomal sclerite, fused posterolaterally to apices of parastomal bars or indistinct and fused to anterodorsal part of hypostomal sclerite. Hypostomal sclerite H-shaped in dorsal or ventral view; sensory plate between anterior rami pigmented and with windows; dorsolateral plate-like extensions of rami forming dorsally open trough. Praryngeal sclerites not joined anterodorsally by dorsal bridge; no pharyngeal ridges between margins of pharyngeal sclerites.

First-instar larva (Fig. 5-8, 35, 36). — Length 0.9-4.0 mm, greatest width 0.3-1.6 mm. White; integument transparent; with dense coat of minute, transparent conical spinules. Integumentary processes (recurved spinules on ventral tubercles of middle ring, hooks on anal proleg, interspiracular hairs, and bristles and spinules of posterior spiracular disc) relatively much larger than in second or third instar, indicating that the first-instar larva is more active or that locomotion is more dependent on some of these structures during the first stadium. Outer pair of ventral tubercles on middle rings of VI-XI each with 1 long, fine, basally darkened bristle in middle of spinule patch. Metapneustic. Each spiracular plate with B-shaped opening. Each lobe of posterior spiracular disc terminating in 1 long, fine bristle.

Cephalopharyngeal skeleton length 0.322-0.406 mm, indentation index 33-52. Accessory teeth absent. Ventral ramus of mouthhook bicuspid apically; anterior cusp larger than posterior cusp. Posterior rami of hypostomal sclerite fused to pharyngeal sclerite. (Based on : *K. albiseta* (SCOPOLI), *K. lineata* (FALLÉN), *K. trifaria* (LOEW), *K. turcestanica* (HENDEL), and *K. unipunctata* (MACQUART).

Second-instar larva (Fig. 9, 10, 26, 31, 32, 34, 37). — Length 3.6-7.2 mm, greatest width 0.8-1.6 mm. Integument translucent; young larvae unicolorous gray, older larvae pigmented as in third instar; with dense coat of minute, subtriangular, brownish, scale-like spinules (Fig. 32). Outer pair of ventral tubercles on middle ring of VI-XI with 1 short, fine, basally darkened bristle in middle of spinule patch. Amphineustic. Anterior spiracules with rudimentary papillae; basal portion slightly swollen proximally, 1.5-4 times as long as apical portion; internal rod-like structures not evident. Posterior spiracular disc with dense coat of minute, elongate spinules (indistinct below 100 ×). Spiracular tubes 0.125-0.200 mm long, divergent, light brown, rugose. Spiracular plates dark, shiny, slightly wider than apices of spiracular tubes; 3 yellow spiracular slits, radially arranged, curved over margin of plate; interspiracular hairs extending slightly beyond bases of spiracular tubes.

Cephalopharyngeal skeleton length 0.574-0.760 mm, indentation index 38-50. Hook-part of mouthhook strongly decurved; 2-5 lightly pigmented, decurved accessory teeth on lightly pigmented anteroventral margin of mouthhook below hookpart; posterodorsal process of basal part longer than posteroventral process. Anterior margin of ventral arch with 24-26 teeth; posterior portion symmetrically bilobed, each lobe with window. Posterior rami of hypostomal sclerite fused to pharyngeal sclerite. Ventral cornua of pharyngeal sclerite with window; dorsal cornu without window. (Based on *K. albiseta* (SCOPOLI), *K. trifaria* (LOEW), *K. turcestanica* (HENDEL), and *K. unipunctata* (MACQUART).

Third-instar larva (Fig. 11-25, 27-29, 33, 38). — Length 10.4-12.0 mm, greatest width 1.8-2.6 mm. Integument translucent; with dense coat of minute, scale-like spinules. Segments I and II, posterior surface of anal proleg, perianal pad, and dome-like swellings supporting posterior spiracular tubes white; remaining surface straw-yellow with pattern of tan longitudinal stripes dorsally and short rows of lightly infuscated punctations (points of muscle attachment) on all sides. Color pattern : dark tan, irregular, mid-dorsal stripe between inner dorsal tubercles extending from anterior margin of V to posterior margin of XI, bordered by slightly shorter inner pair of unpigmented stripes and outer pair of pigmented stripes. Amphineustic. Anterior spiracles with 16-27 closely, regularly arranged papillae on elongate apical portion; discal area of apical portion with many fine, transverse, internal, rod-like structures (appearing externally as prismatic areas); papillae with many fine pores distally. Posterior spiracular disc with dense coat of minute, elongate spinules (indistinct below 100 ×).

Cephalopharyngeal skeleton length 0.96-1.20 mm; indentation index 35-46. Four to 6 lightly pigmented, decurved accessory teeth on lightly pigmented antero-ventral margin of mouthhook below hook part; 1 large ventral window in basal part; posterodorsal process of basal part longer than posteroventral process. Ventral arch with 21-26 teeth on anterior margin; posterior portion symmetrically bilobed, each lobe with window; 1 pair of small approximate windows on medial connection. Epistomal sclerite with 2 pairs of windows anteromesally; no posterior lobes. Plate between anterior rami of hypostomal sclerite with 2 pairs of subequal windows, ligulate sclerite joined to plate by lightly pigmented connection. Hypostomal sclerite with or without cross-bar between posterior rami; separate from pharyngeal sclerites. Dorsal cornua equal in length or much longer than ventral cornua, without window; ventral cornua usually with distinct window. (Based on larvae of *K. trifaria* (LOEW), *K. turcestanica* (HENDEL), and *K. unipunctata* (MACQUART) and puparia of *K. albiseta* (SCOPOLI), *K. corcyrensis* VERBEKE and *K. lineata* (FALLÉN).

Puparium (Fig. 39-50). — Length 6.80-8.53 mm, greatest width 2.20-4.00. Reddish-orange or different shades of brown with various kinds of pruinosity or luster; pattern of longitudinal middorsal stripes present in most species. Integument opaque, that of most species wrinkled or shagreened. Elongae, robust; anterior end dorsoventrally flattened and apically truncate; posterior end tapered. Dorsoventrally asymmetrical; ventral surface strongly arched dorsally at both ends; dorsal surface almost flat to strongly convex at mid-length. Anterior spiracles arising from anterolateral angle of dorsal cephalic cap, 0.196-0.644 mm long; darkly pigmented, conico-elongate basal portions directed anterodorsally, divergent and bearing lightly pigmented, flat apical portion with 16-37 closely set, marginal papillae, the papillae not as regularly arranged as in the larval stage. Segment I and anterior portion of II invaginated. III with 2 pairs of diagonal grooves on dorsolateral and ventrolateral surfaces; IV and V with stronger grooves forming lateral ridge along lateral suture between cephalic caps. Anal proleg barely to conspicuously protuberant; with many large, recurved spinules. Peri-anal pad invaginated. Postanal portion of XII moderately elongate, strongly tapered, upturned at approximately 45-degree angle from longitudinal axis of puparium, raising posterior spiracles higher than anterior spiracles in most species. Vestiges of dorsolateral and lateral lobes of posterior spiracular disc poorly developed; vestiges of ventrolateral and ventral lobes well developed; middle area of disc inflated and bearing spiracular tubes. Interspiracular hairs appressed to spiracular tubes and not obvious in dry specimens.

Knutsonia albiseta (SCOPOLI)

Egg. (Fig. 4). — Length 1.90 - 2.00 mm, greatest width 0.50 - 0.60 mm. Anterior lip equal in length to short posterior tubercle. (Based on 15 specimens : Overmeire, Belgium).

First-instar larva. (Fig. 6). — Length 1.8 - 3.0 mm, greatest width 0.4 - 0.7 mm. Cephalopharyngeal skeleton length 0.364 - 0.406 mm, indentation index 35 - 40. Hookpart of mouthhook strongly decurved; ventral ramus darkly pigmented. Hypostomal sclerite and dorsal cornua of pharyngeal sclerite not exceptionally long. (Based on 10 specimens : Overmeire, Belgium).

Second-instar larva. (Fig. 9, 31, 32, 34). — Integumentary scales short (Fig. 32). Anterior spiracle with 10 - 15 papillae, basal portion 4 times as long as apical portion. Ventrolateral and ventral lobes slightly more than 8 times length of lateral lobes. No indication of segmentation of ventrolateral lobes; ventrolateral and ventral lobes widely separate; ventral lobes slightly connate basally.

Cephalopharyngeal skeleton length 0.625 - 0.760 mm, indentation index 49. Hook-part of mouthhook strongly decurved; no notch in dorsal margin; 3 accessory teeth. Ventral arch with 24 -26 teeth. Hypostomal and pharyngeal sclerites completely fused. Reticulate pattern in lower part of pharyngeal sclerite distinct; dorsal and ventral cornua of pharyngeal sclerite subequal in length. (Based on 5 specimens; Overmeire, Belgium).

Third-instar larva. (Fig. 11, 15, 16, 18). — Anterior spiracles with 19-22 papillae. Posterior spiracular tubes 0.200 mm long; interspiracular hairs extending to bases of tubes. Hooks on anal proleg as in Figure 31.

Cephalopharyngeal skeleton length 1.05 - 1.20 mm, indentation index 35 - 46. Accessory teeth 4 - 5, elongate, rather widely spaced. Ventral arch with 21 - 26 teeth. No cross-bar between posterior rami of hypostomal sclerite. Dorsal cornu of pharyngeal sclerite slightly longer than ventral cornu; window in ventral cornu distinct. (Based on 25 specimens, *ex* puparium : Overmeire, Belgium; Lazio, Italy; Corfu, Greece).

Puparium. (Fig. 40, 43). — Length 7.5 - 8.5 mm, greatest width 3.1 - 4.0 mm. Light greyish-brown to dark reddish-brown, with fine, golden pruinosity. Middorsal brown stripe bordered by inner pair of broad, grey stripes and outer pair of brown stripes. II reddish-brown. Integument with strong transverse wrinkles on dorsal and lateral surfaces, especially anteriorly and posteriorly; surface of non-wrinkled areas pruinose and often shagreened. Anterior spiracles extending slightly above dorsal surface of puparium, 0.238 - 0.294 mm long; basal portion shiny reddish-brown, almost twice as long as apical portion; apical portion ovate, external surface brownish, 19 - 22 papillae. Dorsal surface convex. Sinuous dorsolateral ridge indistinct. Only ventral tubercle vestiges distinct. Anal proleg slightly protuberant. Lateral tubercle above proleg prominent. Postanal portion of XII elongate, narrow. Posterior spiracles above anterior spiracles. Ventrolateral and ventral lobe vestiges of posterior spiracular disc almost reaching posterior margin of anal proleg. Inflated middle area of disc reddish or piceous; pruinose; not apically bifurcated. (Based on 25 specimens : Overmeire, Belgium; Lazio, Italy; Corfu, Greece).

Knutsonia corcyrensis VERBEKE

Third-instar larva. (Fig. 19). — Anterior spiracles with 17 papillae. Posterior spiracular tubes 0.200 mm long; interspiracular hairs extending to bases of tubes.

Cephalopharyngeal skeleton similar to *K. albiseta* (SCOPOLI); length 1.02 - 1.06 mm, indentation index 40 - 43. Accessory teeth 4, very strongly recurved, short, on strongly protruding basis, uppermost tooth half as large as others. Ventral window in basal part of mouthhook much larger than that of *K. albiseta* (SCOPOLI), surrounding area more lightly pigmented; posterodorsal process broader than in *K. albiseta* (SCOPOLI). Plate between anterior rami of hypostomal sclerite narrower than that of *K. albiseta* (SCOPOLI); no cross bar between posterior rami. Dorsal cornua of pharyngeal sclerite slightly longer than that of *K. albiseta* (SCOPOLI) but shorter than that of *K. unipunctata* (MACQUART); dorsal border rather wide; window in ventral cornua distinct. (Based on 25 specimens *ex* puparium : Corfu, Greece).

Puparium. (Fig. 41, 44). Length 7.40 - 8.20 mm, greatest width 2.60 - 3.04 mm. Golden-brown with coarse pruinosity; diffuse light tan to brown middorsal stripe bordered by inner pair of broad, yellowish or greenish-white stripes and outer pair of narrow, dark brown stripes extending from V to anterior margin of XII. II shiny, reddish-brown. Shape similar to *K. albiseta* (SCOPOLI), relatively longer and thinner. Integument with moderately strong wrinkles dorsally and laterally at anterior and posterior ends, remaining surface sparsely wrinkled and coarsely pruinose. Anterior spiracles extending above dorsal surface of puparium, 0.196 - 0.266 mm long; basal portion only slightly longer than apical portion; apical portion ovate, shiny reddish-black; 17 papillae. Dorsal surface strongly convex, outline sinuous. No dorsolateral ridge. Anal proleg slightly protuberant. Lateral tubercle above proleg indistinct. Post-anal portion of XII elongate, narrow. Posterior spiracles above anterior spiracles. Ventrolateral and ventral lobe vestiges of posterior spiracular disc with lightly colored pruinosity, almost reaching posterior margin of anal proleg. Inflated middle area of disc piceous, pruinose, not apically bifurcated. (Based on 44 specimens : Corfu, Greece).

Knutsonia trifaria (LOEW)

Egg. — Length 1.16 - 1.26 mm, greatest width 0.38 - 0.40 mm. Anterior lip shorter than small posterior tubercle. (Based on 30 specimens : Rioja, Spain).

First-instar larva. (Fig. 36). — Length 1.6 - 3.6 mm, greatest width 0.4 - 0.8 mm. Dorsolateral and lateral lobes of posterior spiracular disc indistinct; ventrolaterals and ventrals elongate, subequal, connate basally; ventrolaterals not segmented; ventrals widely spaced.

Cephalopharyngeal skeleton similar to *K. albiseta* (SCOPOLI); length 0.350 - 0.378 mm, indentation index 36 - 40. Central area of pharyngeal sclerite slightly shorter than in *K. albiseta* (Scopoli). (Based on 25 specimens : Adra, Spain).

Second-instar larva. (Fig. 37). — Length 4.0 - 6.0 mm, greatest width 0.9 - 1.4 mm. Integumentary scales elongate. Anterior spiracles with 20 papillae; basal portion 1.5 times as long as apical portion.

Cephalopharyngeal skeleton similar to *K. albiseta* (SCOPOLI); length 0.574 - 0.658 mm, indentation index 38 - 43. Hook-part of mouthhook not as decurved as in *K. albiseta* (SCOPOLI), distinct notch in dorsal margin before irregular connection. Accessory teeth 3 - 4; short, blunt projection below lower tooth more distinct than in *K. albiseta* (SCOPOLI). Hypostomal and pharyngeal sclerites completely fused. Dorsal and ventral cornua of pharyngeal sclerite sub-equal in length. (Based on 25 specimens : Adra, Spain).

Third-instar larva. (Fig. 22, 27, 38). — Length 11.2-12.0 mm, greatest width 1.8 - 2.6 mm. Anterior spiracles with 19 - 23 papillae; proximal pair of papillae slightly supramarginal; apical portion longer than basal portion. Outer dorsal dark stripe twice as wide as middorsal dark stripe; no continuous dark stripe between dorsolateral tubercle and upper tubercle of lateral group; XII not darkly pigmented. Dorsolateral and lateral lobes of posterior spiracular disc short, hemispherical; ventrolateral and ventral lobes about 8 times length of dorsolateral lobes; relatively shorter than in I or II instar (indicating a less aquatic existence during III stadium). Ventrolateral and ventral lobes slightly connate basally; ventrals widely separate. Posterior spiracular tubes 0.150 mm long; interspiracular hairs extending almost to bases of tubes.

Cephalopharyngeal skeleton similar to *K. albiseta* (SCOPOLI); length 0.96 - 1.12 mm, indentation index 38 - 46. Four to 5 closely set, thin accessory teeth on strongly posteriorly sloping anterior margin of basal part (1 specimen taken from puparium with only 1 accessory tooth on 1 side). Ventral arch with 26 teeth. Anteromesal margin of epistomal sclerite elongate. Hypostomal sclerite with lightly pigmented bar between posterior rami. Dorsal cornua of pharyngeal sclerite with broad border, slightly larger than ventral cornua. Window in ventral cornua distinct. (Based on 25 specimens : Adra, Spain).

Puparium. (Fig. 46, 49). — Length 6.8 - 7.2 mm, greatest width 2.4 - 2.8 mm. Greyish-brown with golden-tan pruinosity; diagonal black marks in dorsolateral depressions; diffuse middorsal brown stripe bordered by inner pair of broad light stripes and outer pair of narrow dark stripes extending from anterior margin of IV to posterior margin of XI. II piceous. III pruinose, reddish-brown. Integument wrinkled only along primary and secondary folds; areas between folds pruinose and occasionally shagreened. Anterior spiracles below dorsal surface of puparium, 0.280 - 0.350 mm long; basal portion piceous, conical, half as long as apical portion; apical portion ovate, yellow, 1,5 - 2 times as long as width at midlength; 19 - 23 papillae. Dorsal surface moderately convex. Sinous dorsolateral ridge strongest anteriorly. Anterodorsal tubercle vestiges represented by faint pruinose areas, ventral tubercle vestiges distinct. Anal proleg moderately to strongly protuberant. Lateral tubercle above proleg distinct. Postanal portion of XII short, broad. Posterior spiracles above anterior spiracles. Ventral spiracular disc lobes extending beyond posterior margin of anal proleg. Inflated middle area of disc brownish and pruinose basally; bifurcations slightly inflated, reddish-orange, pruinose. (Based on 41 specimens : Adra, Spain).

Knutsonia turcestanica (HENDEL)

Egg. — Length 1.02 - 1.12 mm, greatest width 0.29 - 0.31 mm. Anterior lip shorter than small posterior tubercle. (Based on 16 specimens : Gerani, Crete).

First-instar larva. — Length 1.6 - 4.0 mm, greatest width 0.4 - 0.8 mm. Posterior spiracular disc as in *K. trifaria* (LOEW).

Cephalopharyngeal skeleton similar to *K. albiseta* (Scopoli); length 0.322- 0.364 mm, indentation index 33 - 43. Hook-part of mouthhook not as strongly decurved as in *K. albiseta* (Scopoli). (Based on 25 specimens : Gerani, Crete).

Second-instar larva. — Length 4.0 - 7.2 mm, greatest width 0.8 - 1.6 mm. Integumentary scales elongate. Anterior spiracles with 30 - 35 papillae; basal portion 1.5 times as long as apical portion. Posterior spiracular disc as in *K. trifaria* (Loew).

Cephalopharyngeal skeleton similar to *K. albiseta* (Scopoli); length 0.602 - 0.644 mm, indentation index 35 - 43. Hook-part of mouthhook strongly decurved, as in *K. albiseta* (Scopoli), notch in dorsal margin deeper than in *K. trifaria* (Loew); hook-part thicker basally than in all other species; 3 - 5 accessory teeth, not as regular in shape, number, or position as in *K. albiseta* (Scopoli) or *K. trifaria* (Loew); lower-most accessory tooth blunt, lobe-like in some specimens. Anterior margin of epistomal sclerite convex, hyaline. Hypostomal and pharyngeal sclerites completely fused. Dorsal and ventral cornua of pharyngeal sclerite subequal in length. (Based on 25 specimens : Gerani, Crete).

Third-instar larva. (Fig. 21, 24, 25, 27). Length 10.4 - 12.0 mm, greatest width 1.8 - 2.4 mm. Anterior spiracles with 33 - 37 papillae; apical portion longer than basal portion. Posterior spiracular tubes 0.150 mm long; interspiracular hairs extending to bases of tubes. Posterior spiracular disc as in *K. trifaria* (Loew). Outer dorsal dark stripe equal in width to middorsal dark stripe; no continuous dark stripe between dorsolateral tubercle and upper tubercle of lateral group. XII not darkly pigmented.

Cephalopharyngeal skeleton similar to *K. albiseta* (Scopoli); length 1.00 - 1.02 mm, indentation index 37 - 44. Four to 6 closely set, strongly recurved accessory teeth on strongly sloping anterior margin of basal part, teeth on ventral arch exceedingly small. Anterior margin of epistomal sclerite hyaline. No cross bar between posterior rami of hypostomal sclerite. Dorsal and ventral cornua of pharyngeal sclerite subequal in length. Window in ventral cornua distinct. (Based on 25 specimens : Gerani, Crete).

Puparium. (Fig. 47, 50). — Length 6.9 - 8.0 mm, greatest width 2.2 - 2.7 mm. Reddish-brown, golden pruinose, diagonal black marks in dorsolateral depressions; broad middorsal brown stripe extending from anterior margin of IV to posterior margin of XI, bordered by faint inner light stripe and outer dorsal brown stripe. II shiny, black. III reddish, pruinose. Integument wrinkled only along primary and secondary folds, areas between folds pruinose or shagreened. Anterior spiracles extending to or sligthly above dorsal surface of puparium, 0.490 - 0.644 mm long; basal portion shiny, brown, half as long as apical portion; apical portion lanceolate, yellow; 33 - 37 papillae. Dorsal surface moderately convex.

Sinuous dorsolateral ridge prominent anteriorly. Dorsal tubercle vestiges represented by pruinose areas. Ventral tubercle vestiges moderately distinct. Anal proleg slightly to strongly protuberant. Lateral tubercle above proleg distinct. Postanal portion of XII short, broad. Posterior spiracles extending slightly above dorsal surface and anterior spiracles. Ventrolateral and ventral lobe vestiges of posterior spiracular disc extending almost to posterior margin of anal proleg. Inflated middle area of disc reddish-brown, pruinose, bifurcated; bifurcations strongly swollen. (Based on 35 specimens : Gerani, Crete.)

Knutsonia unipunctata (MACQUART)

Egg. — Length 1.10 - 1.20 mm, greatest width 0.28 - 0.33 mm. Anterior lip shorter than small posterior tubercle. (Based on 13 specimens : Tijola, Spain).

First-instar larva. (Fig. 7). — Length 0.9 - 2.2 mm, greatest width 0.6 - 1.6 mm. Spinules on ventral tubercles of middle ring very well-developed. Hooks on anal proleg longer and narrower than in other species. Lobes of posterior spiracular disc shorter than in other species. Dorsolateral lobes indistinct; lateral lobes short, conical, 1/2 as long as ventrolaterals; ventrolaterals slightly 2-segmented; ventrolaterals and ventrals subequal, not connate basally; ventral lobes connate basally.

Cephalopharyngeal skeleton length 0.392 - 0.406 mm, indentation index 47 - 52. Hook-part of mouthhook strongly decurved, broader than in other species. Central area of pharyngeal sclerite as long as that of *K. albiseta* (SCOPOLI); dorsal cornua dark, much longer and narrower than ventral cornua. (Based on 25 specimens : Tijola Spain).

Second-instar larva. (Fig. 10). — Length 3.6 - 7.2 mm, greatest width 0.8-1.4 mm. Scale-like spinules of integument fine and sharply pointed; spinules of III large. Anterior spiracles with 21-25 papillae; basal portion 3 times as long as apical portion. Ventrolateral lobes slightly 2-segmented; ventral lobes connate basally for short distance. Apices of spiracular disc lobes with very long spinules; transparent bristles near middle of ventrolateral and ventral lobes longer than in other species.

Cephalopharyngeal skeleton length 0.588-0.644 mm, indentation index 44-50. Hook part of mouthhook not as decurved as in *K. albiseta* (SCOPOLI); notch in dorsal margin shallow or absent; 2-3 accessory teeth. Hypostomal sclerite narrowly joined to pharyngeal sclerite ventromedially. Dorsal cornua of pharyngeal sclerite strongly tapered, much longer and narrower than ventral cornua. Window in ventral cornua indistinct. (Based on 25 specimens : Tijola, Spain).

Third-instar larva..(Fig. 12, 16, 23, 28, 33). — Length 11.5-12.0 mm, greatest width 1.9-2.5 mm. Outer dorsal dark stripe 4 times as

broad as middorsal dark stripe, extending from lateral edge of inner dorsal tubercle to mesal edge of dorsolateral tubercle; light stripe along dorsolateral tubercles and continuous dark stripe between dorsolateral tubercle and upper tubercle of lateral group; XII darkly pigmented. Anterior spiracle with 22-26 papillae; proximal pair distincly supramarginal; apical portion shorter than basal portion. Posterior spiracular tubes 0.150 mm long; interspiracular processes extending to bases of tubes, each consisting of 5 main trunks terminating in about 50 points (Fig. 30). Posterior spiracular disc (Fig. 33). Ventrolateral and ventral lobes short, triangular, slightly longer than dorsolateral lobes. Ventral lobes slightly connate basally.
Cephalopharyngeal skeleton length 0.90-1.00 mm, indentation index 43-46. Hook-part of mouthhook broader and slightly straighter than in other species; 3-4 elongate, broad accessory teeth; lowermost tooth much smaller than others. Ventral arch with 24 minute teeth. Hypostomal sclerite with darkly pigmented cross bar between posterior rami. Dorsal cornua much longer and narrower than ventral cornua. Window in ventral cornua indistinct. (Based on 25 specimens : Tijola, Spain).

Puparium. (Fig. 39, 42). — Length 2.6-7.4 mm, greatest width 2.2-2.5 mm. Reddish-brown to piceous-brown, with very faint pattern of dorsal stripes. Integument of VI-XI moderately wrinkled dorsally and weakly wrinkled laterally and ventrally, with yellowish pruinosity on smoother areas. II-V and XII pruinose. Anterior spiracles extending to or above dorsal surface of puparium, 0.280-0.378 mm long, basal portion shiny, piceous-brown, equal in length to apical portion; external surface of apical portion ovate, brown; 22-26 papillae. Dorsal surface barely convex. Sinuous dorsolateral ridge indistinct. Only dorsolateral tubercle vestiges of XI and ventral tubercle vestiges of other segments distinct. Anal proleg not protuberant. Lateral tubercle above proleg distinct. Postanal portion of XII relatively short, broadly conical. Posterior spiracles extending above dorsal surface of puparium and above anterior spiracles. Ventrolateral and ventral lobe vestiges of posterior spiracular disc very short. Inflated middle area of disc reddish, bifurcated; bifurcations strongly divergent, not swollen. (Based on 7 specimens : Tijola, Spain).

Knutsonia lineata (FALLÉN)

Egg. — Length 0.88-1.36 mm, greatest width 0.27-0.37 mm. Apices more acute than in other species. Anterior lip almost as long as elongate posterior tubercle. (Based on 26 specimens : Lake Erken, Sweden, 10; Suserup, Denmark, 16).

First-instar larva. (Fig. 8, 35). — Length 1.6-2.1 mm, greatest width 0.3-0.4 mm. Two pair of dorsal and 2 pair of lateral lobe-like tubercles on VI-XI becoming longer posteriorly; lobes on X and XI distinctly longer than any other described species of *Sciomyzidae*. Inner dorsal lobe longer than outer dorsal, upper lateral lobe longer than lower lateral. Hooks on inner pair of ventral tubercles of middle ring much larger and darker than in other species of the genus, hooks on outer pair only slightly recurved. Posterior spiracular disc with paired, low, hemispherical dorsal lobes and elongate lateral, ventrolateral, and ventral lobes. Ventral and ventrolateral lobes subequal, lateral lobe 1/8 shorter. Anal proleg with 3 rows of hooks. Interspiracular hairs much shorter than those of other species in the genus. Spiracular tubes and plates lightly pigmented, very small.

Cephalopharyngeal skeleton length 0.336-0.364 mm, indentation index 33. Hookpart of mouthhook narrow and only slightly decurved; ventral ramus lightly pigmented. Hypostomal sclerite as long as pharyngeal sclerite, darkly pigmented, narrowed anteriorly. Dorsal cornua and central area of pharyngeal sclerite short. (Based on 15 specimens : Lake Erken, Sweden).

Third-instar larva. (Fig. 13, 14, 20). — Anterior spiracles with 16 papillae. Posterior spiracular tubes conico-elongate, 0.125 mm long.

Cephalopharyngeal skeleton length 0.90 mm, indentation index 43. Accessory teeth 5, small, very lightly pigmented, strongly decurved. Epistomal sclerite indistinct, fused to anterodorsal part of hypostomal sclerite. Hypostomal sclerite almost as long as pharyngeal sclerite, darkly pigmented ventrally, dorsolateral extensions lightly pigmented; broad and darkly pigmented parastomal bars fused to dorsal margin; central cross bar very long and with weak median line; posterior rami short, without cross-bar. Parastomal bars extending anteriorly almost as far as anterior margin of hypostomal sclerite, fusion with pharyngeal sclerite narrow and lightly pigmented. Dorsal and ventral cornua of pharyngeal sclerite subequal in length. Window in ventral cornua distinct. (Based on 1 specimen, *ex puparium* : Suserup, Denmark).

Puparium. (Fig. 45, 48). — Length 6.4 mm, greatest width 2.0 mm. Uni-colorous reddish-orange, tubercle vestiges and XII piceous. Integument not wrinkled; with dense, uniform coat of small spinules. Anterior spiracles extending above dorsal surface of puparium, 0.24 mm long; basal portion elongate, shiny-orange; apical portion lanceolate, external surface yellow; 16 papillae. Dorsal surface flat. XII strongly tapered posteriorly, center of spiracular disc below dorsal surface of puparium. V-XI each with 2 pairs of dorsal, 2 pairs of dorsolateral, and 2 pairs of ventral lobe vestiges on each side, lobes progressively larger on each succeeding segment toward posterior end. Ventral lobes with short, posteriorly recurved spinules. No sinuous dorsolateral ridge. Anal proleg barely protuberant. Lateral tubercle vestige above proleg distinct. Ventrolateral and ventral lobe vestiges of posterior spiracular disc extending to anal proleg. Inflated middle area of disc bifurcated apically, bifurcations conico-elongate. Posterior spiracles slightly below dorsal surface of puparium. (Based on 1 specimen : Suserup, Denmark).

Key to Third-instar Larvae

1. Elongate tubercles on segments V-XI; integument heavily spinulose; 16 anterior spiracle papillae; hypostomal sclerite 4 times as long as wide (Fig. 14). Central and northern Europe . *K. lineata* (FALLÉN)

— No elongate tubercle on V-XI; integument smooth; 17-37 papillae; hypostomal sclerite quadrate (as Figs. 16, 17) 2

2. Ventral and ventrolateral lobes of posterior spiracular disc only slightly longer than wide (Fig. 33); middorsal stripe indistinct; dorsal cornu of pharyngeal sclerite much longer than ventral cornu (Fig. 12); window in ventral cornu indistinct (Fig. 12). Western Mediterranean . . . . *K. unipunctata* (MACQUART)

— At least ventral and ventrolateral lobes much longer than wide (as Fig. 34); middorsal stripe distinct (as Fig. 25); dorsal and ventral cornua subequal (as Figs. 11, 13); window in ventral cornu distinct (as Figs. 11, 13) 3

3. Anterior spiracles elongate, 33-37 papillae (Fig. 29). Eastern Mediterranean, central Asia . . . . *K. turcestanica* (HENDEL)

— Anterior spiracles relatively short, 17-23 papillae (as Figs. 27, 28) . 4

4. Cross-bar between posterior rami of hypostomal sclerite (Fig. 17). Western Mediterranean . . . . *K. trifaria* (LOEW)

— No cross-bar (as Fig. 16) 5

5. Integument finely pruinose; accessory teeth subequal (Fig. 18). Throughout Europe . . . . *K. albiseta* (SCOPOLI)

— Integument coarsely pruinose; uppermost accessory tooth half as large as others (Fig. 19). Endemic to Corfu, Greece ? . . . . *K. corcyrensis* VERBEKE

Key to Puparia

1. Elongate tubercle vestiges on segments V-XI; integument not wrinkled, spinulose; dorsum flat; center of posterior spiracular disc below dorsal surface of puparium (Fig. 45, 48). Central and northern Europe . . . . *K. lineata* (FALLÉN)

— No elongate tubercle vestiges on V-XI; integument wrinkled, without spinules; dorsum slightly to strongly convex; center of spiracular disc above dorsal surface of puparium 2

2. Dorsum strongly convex at mid-length; postanal portion of XII elongate, narrow; inflated central area of posterior spiracular disc not bifurcated at bases of spiracular tubes 3

— Dorsum weakly or moderately convex; postanal portion of XII short, broad; inflated central area of posterior spiracular disc bifurcated at bases of spiracular tubes 4

3. Twice as long as wide; integument finely pruinose and shagreened, strongly wrinkled; vestiges of ventrolateral and ventral lobes of posterior spiracular disc extending only half-way to posterior margin of anal proleg (Fig. 40, 43). Throughout Europe .*K. albiseta* (Scopoli)

— Three times as long as wide; integument coarsely pruinose, not shagreened, weakly wrinkled; vestiges of ventrolateral and ventral lobes extending almost to posterior margin of anal proleg (Fig. 41, 44). Endemic to Corfu, Greece ? . . . . . . *K. corcyrensis* Verbeke

4. Integument densely wrinkled; dorsum weakly convex; pattern of middorsal stripes faint; vestiges of ventrolateral and ventral lobes of posterior spiracular disc very short; bifurcations of central area of disc not swollen; anal proleg not protuberant (Fig. 39, 42). Western Mediterranean . . . . *K. unipunctata* (Macquart)

— Integument wrinkled only along primary and secondary folds; dorsum moderately convex; pattern of middorsal stripes well-developed; vestiges of ventrolateral and ventral lobes elongate; bifurcations of central area of disc swollen; anal proleg protuberant 5

5. Anterior spiracles elongate (0.49-0.64 mm), above dorsal surface; strongly divergent, 33-37 papillae; vestiges of ventrolateral and ventral lobes of posterior spiracular disc extending almost to posterior margin of anal proleg (Fig. 47, 50). Eastern Mediterranean, central Asia . . . . *K. turcestanica* (Hendel)

— Anterior spiracles short (0.28-0.35 mm), below dorsal surface; moderately divergent, 19-23 papillae; vestiges of ventrolateral and ventral lobes extending beyond anal proleg (Fig. 46, 49). Western Mediterranean . . . . *K. trifaria* (Loew)

DISCUSSION

Intrageneric Relationships

On the basis of morphological features of the adults and geographical distribution, Verbeke (1964) placed *K. trifaria* (Loew) and *K. turcestanica* (Hendel) in the *trifaria* group, and *K. unipunctata* (Macquart), *K. truquii* (Rondani) and *K. corcyrensis* Verbeke in the *unipunctata* group. *Knutsonia albiseta* (Scopoli) was regarded as distinct from these species groups. *K. lineata* (Fallén) and *K. rossica* (Mayer), appeared together in the first couplet of the key and were referred to as showing, « ... nombreux caractères aberrants par rapport aux autres *Knutsonia*... ». Utilizing the data and some conclusions presented by Verbeke (1964) and biological and morphological knowledge of the immature stages, we propose the following arrangement.

Subgenus Knutsonia, typical subgenus
Type-species, *Musca albiseta* Scopoli, 1763

albiseta group

albiseta (Scopoli), 1763	*corcyrensis* Verbeke, 1964

unipunctata group

unipunctata (Macquart), 1849	*truquii* (Rondani), 1863

trifaria group

trifaria (Loew), 1847	*turcestanica* (Hendel), 1903

Subgenus Tumidicercus, new subgenus
Type-species, *Tetanocera lineata* Fallén, 1821.

lineata (Fallén), 1821	*rossica* (Mayer), 1953

Characteristics of the Subgenus *Knutsonia* and the Species Groups

Adults of the subgenus *Knutsonia* are characterized by the following features : prosternum mostly bare; prescutellar acrostical bristles well developed; micro-bristles well developed; cerci of male not atypically inflated. Third-instar larvae (of the five reared species; *K. truquii* (Rondani) is unknown) have a well developed epistomal sclerite; the parastomal bars are of normal size; the hypostomal sclerite is quadrate; the hypostomal and pharyngeal sclerites are not fused; body tubercles are not elongate; and the integument is furnished with minute, scale-like spinules. The posterior spiracles of the puparia are situated above the anterior spiracles.

Members of the typical group (*K. albiseta* (Scopoli) and *K. corcyrensis* Verbeke) are similar in being the only species of the subgenus having an entirely white arista, in having similar male genitalia, and well developed vallar bristles. The cephalopharyngeal skeleton and puparia are more similar to each other than either is to any other member of the subgenus. Both species seem to be univoltine, whereas other species of the subgenus are multivoltine. Verbeke (1964) placed *K. corcyrensis* Verbeke in his « groupe *unipunctata* » (*K. unipunctata* (Macquart), *K. truquii* (Rondani) and *K. corcyrensis* Verbeke) and used the following characters to distinguish this group from *K.*

albiseta (SCOPOLI) : arista plumose, second and third antennal segments shorter than greatest diameter of eye, costal margin of wing not darkened, abdomen with dark middorsal stripe, fifth tergite of male abdomen elongate, and ninth tergite without a pair of small anal tubercles.

Similarities between adults of our *unipunctata* group *(K. unipunctata* (MACQUART) and *K. truquii* (RONDANI) are found mainly in the male and female genitalia, and the fact that the aristae are plumose and almost entirely black. The larvae of *K. truquii* (RONDANI) are not known but those of *K. unipunctata* (MACQUART) are distinct from other larvae of the subgenus in having exceptionally long dorsal cornua of the pharyngeal sclerite, no windows in the ventral cornua, and short lobes on the posterior spiracular disc. The puparium lacks a middorsal stripe and the shape is distinct from all others of the subgenus. The larvae of *K. unipunctata* (MACQUART) are not as overtly predaceous as other species.

The very similar morphology of the male genitalia is the most obvious character for associating adults of the *trifaria* group (K. *trifaria* (LOEW) and *K. turcestanica* (HENDEL)). Unlike other members of the subgenus, the ventral spinules of the hind femora of the male are not well developed, the vallar bristles are hair-like, and the mesopleural and pteropleural hairs are long and regular. The posterior spiracular discs and puparia also are very similar. The puparia are the only representatives of the subgenus having a strongly protrudent anal proleg.

Characteristics of the Subgenus *Tumidicercus* subgen. nov.

Adults of *Tumidicercus* subgen. nov. have hairs over the entire surface of the prosternum, the prescutellar acrostical bristles are weak, and the cerci of the male are atypically inflated. Larvae of *K. lineata* (FALLÉN) are characterized by the following features : epistomal sclerite weakly developed; parastomal bars extremely long and thick; hypostomal sclerite four times as long as wide; hypostomal and pharyngeal sclerites fused; many body tubercles atypically elongate; and integument heavily spinulose. The posterior spiracles of the puparium are situated below the anterior spiracles.

Possible Evolutionary History

Speculation on the evolutionary history of the genus *Knutsonia* is based on data given in proceeding sections concerning the morphology of the immature stages as well as adults, biology (especially seasonal aspects), and geographical distribution of five of the seven species in the genus. Only the morphology of the adults and limited distributional data are available for *K. rossica* (MAYER) and *K. truquii* (RONDANI), but fortunately, these two seem to be closely related to fairly well known species.

The speculations seem to be most reliable for *K. turcestanica* (HENDEL) and *K. trifaria* (LOEW) (and, if analogous, for *K. truquii* (RONDANI) and *K. unipunctata* (MACQUART), fairly reliable for *K. albiseta* (SCOPOLI) and *K. corcyrensis* VERBEKE, and least reliable for *K. lineata* (FALLÉN) and *K. rossica* (MAYER).

In comparison to other genera of *Tetanocerini*, most of the fundamental morphological and biological features of *Knutsonia* are plesiomorphic or primitive. The present major area of distribution is the western and south central Palearctic. The genus probably arose from a typical tetanocerine stock in the western Palearctic and seems to have diverged along two major lines. One line led to the widespread subgenus *Knutsonia* and the other line led to the apomorphic or derived and restricted subgenus *Tumidicercus* subgen. nov.

The present northern distributions and univoltine life cycles indicate that the subgenus *Tumidicercus* subgen. nov. became strongly adapted to a cold climate. The univoltine life cycles of two central and southern European species of the subgenus *Knutsonia* indicate that adaptation to a cold climate also was characteristic of that subgenus during the earlier stages of its evolution.

The division of the subgenus *Knutsonia* into warm-adapted, multivoltine lines (*trifaria* and *unipunctata* groups) and a somewhat cold-adapted, univoltine line (*albiseta* group) probably occurred before the last glaciation. *Knutsonia albiseta* (SCOPOLI) apparently possessed enough ecological tolerance to remain in southern latitudes after the glacier retreated, and also to follow its retreat and re-invade central (but not far northern) Europe (Fig. 51). *Knutsonia corcyrensis* VERBEKE (apparently univoltine and known only from Corfu) may have evolved from a more strongly cold-adapted segment of populations that became isolated in cooler areas of southeastern Europe. Considering that southeastern Europe has not been extensively collected, the distribution of *K. corcyrensis* VERBEKE may in fact be much more extensive than presently known.

The evolutionary history of the warm-adapted, multivoltine lines of the subgenus *Knutsonia* (groups *trifaria* and *unipunctata*) seems clearer. One of the major glacial advances (perhaps the most recent one) may have pushed a strongly thermophilic ancestral species of the *trifaria* group into the refugia of the Iberian peninsula and the Middle East. The isolated populations of this ancestral form subsequently may have developed into the two closely related species, *K. trifaria* (LOEW) (western Mediterranean) and *K. turcestanica* (HENDEL) (eastern Mediterranean), with recent spread accounting for the presence of *K. turcestanica* (HENDEL) across the southcentral Palearctic (Fig. 52). A similar phenomenon, possibly concurrent with the speciation of *K. trifaria* (LOEW) *and K. turcestanica* (HENDEL), may explain the origin of *K. unipunctata* (MACQUART) (western Mediterranean) and *K. truquii* (RONDANI) (eastern Mediterranean), with the latter species being less successful and presently known only from Damascus (Fig. 52).

Several explanations could be presented for the origin of *K. lineata* (FALLÉN) and *K. rossica* (MAYER), the two synapomorphic species of the cold-adapted subgenus *Tumidicercus* subgen. nov. The more continuous distribution of *K. lineata* (FALLÉN) in northern latitudes than in central Europe indicates that the species is basically cold-adapted but has developed enough ecological tolerance to remain in the moderately diverse area of central and far northern Europe after the glacial front receded (Fig. 51). Populations of *K. rossica* (MAYER) may have been limited to an area near the glacial front and may have followed it in its northward retreat until the species became isolated in its present range (northwestern U. S. S. R.).

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ABSTRACT

Data on the life cycles and on morphology of the immature stages of six of the eight described species of the Palearctic genus *Knutsonia* are presented (*K. albiseta* (SCOPOLI), *K. corcyrensis* VERBEKE, *K. lineata* (FALLÉN), *K. trifaria* LOEW, *K. turcestanica* (HENDEL) and *K. unipunctata* (MACQUART). Larvae of all reared species are predators of aquatic and hygrophilous snails. A sub-generic classification is proposed. Biological and morphological features of the immature stages and adults are utilized in discussions of taxonomic relationships and possible evolutionary history.

TABLE I.

Numbers and dimensions of *Planorbis planorbis* (LINNÉ) killed and eaten by larvae of *K. trifaria* (LOEW), from hatching to pupation (1).

Larva No.	No. eaten in first stadium	No. eaten in second stadium	No. eaten in third stadium	Total no. eaten	Larval life (days)	Pupal Period (Days)	Sex
6404A6-1	11 (0.8-2.0) (2)	12 (1.0-5.2)	12 (2.4-7.2)	35 (0.8-7.2)	25	14	♂
6404A6-2	14 (0.8-1.6)	6 (2.0-3.0)	12 (2.4-6.0)	32 (0.8-6.0)	28	15	♂
6404A6-3	14 (0.8-1.8)	9 (1.0-4.8)	8 (4.8-8.0)	31 (0.8-8.0)	30	died	—
6404A6-4	14 (0.8-1.8)	12 (1.2-4.4)	12 (2.4-7.2)	38 (0.8-7.2)	25	16	♂
6404A6-5	12 (0.8-2.0)	10 (0.8-2.4)	12 (4.0-6.0)	34 (0.8-6.0)	24	15	♂
6404A6-6	9 (0.8-1.8)	10 (1.2-4.0)	13 (2.8-6.8)	32 (0.8-6.8)	25	14	♀
6404A6-7	12 (0.8-2.0)	6 (2.0-3.8)	10 (4.0-7.6)	28 (0.8-7.6)	25	16	♀
6404A6-8	15 (1.8-1.8)	6 (1.6-3.2)	died	—	—	—	—
6404A6-9	12 (0.8-2.2)	9 (1.8-4.8)	11 (4.4-6.4)	32 (0.8-6.4)	22	16	♂
6404A6-10	17 (0.8-2.0)	11 (1.8-4.2)	12 (2.4-6.0)	40 (0.8-6.0)	26	15	♀

(1) The eggs were laid between February 6 and 8, 1964; hatching occurred on February 13; the larvae formed puparia between March 6 and 14; and adults emerged between March 22 and 27.

(2) Range in millimeters of greatest diameter of shells.

TABLE II.

Biological Features of *Knutsonia* spp.

	albiseta	*corcyrensis*	*trifaria*	*turcestanica*	*unipunctata*	*lineata*
Geographical Distribution	Throughout Europe	Corfu, Greece	Western Mediterranean	E. Mediterr., S. W. Asia	Western Mediterranean	N. & C. Europe
Flight Period (1), (2)	E.5-M.11	E.5-?	L.1-L.10	L.3-L.10	L.2-?	L.6-M.10
Preoviposition Period (days) (3)	? 60 +	—	5-10	8	43	? 60 +
Greatest Number of Eggs	375	—	340	211	461	151
Incubation Period (days)	14-45	—	3-7	6-8	6-7	7-20
Stadium I (days)	10	—	6-8	9-11	14-21	—
Stadium II (days)	5-8	—	6-9	7-9	13-16	—
Stadium III (days)	16-20	—	9-15	16-19	19-40	—
Pupal Period (days)	12-42	16 +	14-18	13-15	15-25	—
Duration Immature Stages (days) (4)	? 250 +	—	39-55	51-62	67-107	? 250 +
Pupation Site	water	water	water	water	water	water
Overwintering Stage	larva	—	—	—	—	? larva
Diapause	egg	—	none	none	none	egg
Generations per Year (2)	1	1	5-8	5-6	2-3	1
Maximum Adult Longevity (days)	187	72	109	116	188	137

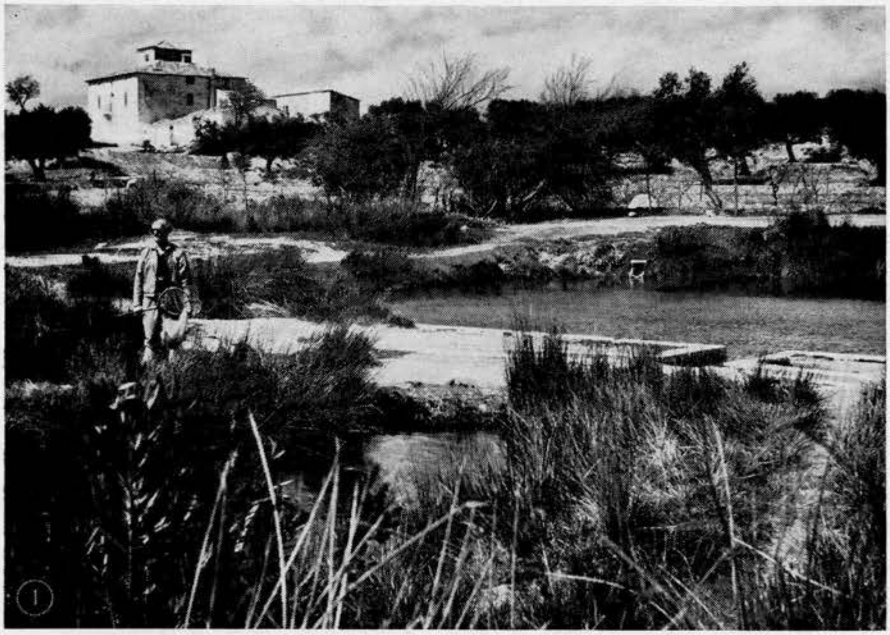
(1) E = early, M = middle, L = late; month indicated by number.
(2) At mid-latitude of range.
(3) Time from emergence until first egg.
(4) Deposition of egg until emergence of adult.

TABLE III.

Morphological Features of Mature Larvae and Puparia of *Knutsonia* spp.

	albiseta	*corcyrensis*	*trifaria*	*turcestanica*	*unipunctata*	*lineata*
Third instar larva :						
no. of accessory teeth	4,5	4	4,5	4-6	3,4	5
epistomal sclerite reduced	—	—	—	—	—	+
parastomal bars massive	—	—	—	—	—	+
HS elongate	—	—	—	—	—	+
HS with posterior cross-bar	—	—	+	—	+	—
hypostomal-pharyngeal fusion	—	—	—	—	—	+
dorsal cornua elongate	—	—	—	—	+	—
VC window distinct	+	+	+	+	—	+
indentation index	35-46	40-43	38-46	37-44	43-46	43
no. of papillae, AS	19-22	17	19-23	33-37	22-26	16
ratio apical/basal portions, AS	0	0	1/1	1/1	2/1	0
some body tubercles elongate	—	—	—	—	—	+
lobes of PSD elongate	+	+	+	+	—	+
Vl & V lobes of PSD connate	—	0	+	+	—	+
V lobes of PSD connate	+	0	—	—	+	—
Puparium :						
integument	wrinkled	wrinkled	wrinkled	wrinkled	wrinkled	spinulose
dorsal stripes	+	+	+	+	—	—
AS above dorsum	+	+	—	+	+	+
PS above AS	+	+	+	+	+	—
anal proleg protuberant	—	—	+	+	—	—

(+ = present; — = absent; 0 = unknown; VC = ventral cornua; AS = anterior spiracle; HS = hypostomal sclerite; PS = posterior spiracle; PSD = posterior spiracular disc; V = ventral; Vl = ventrolateral).



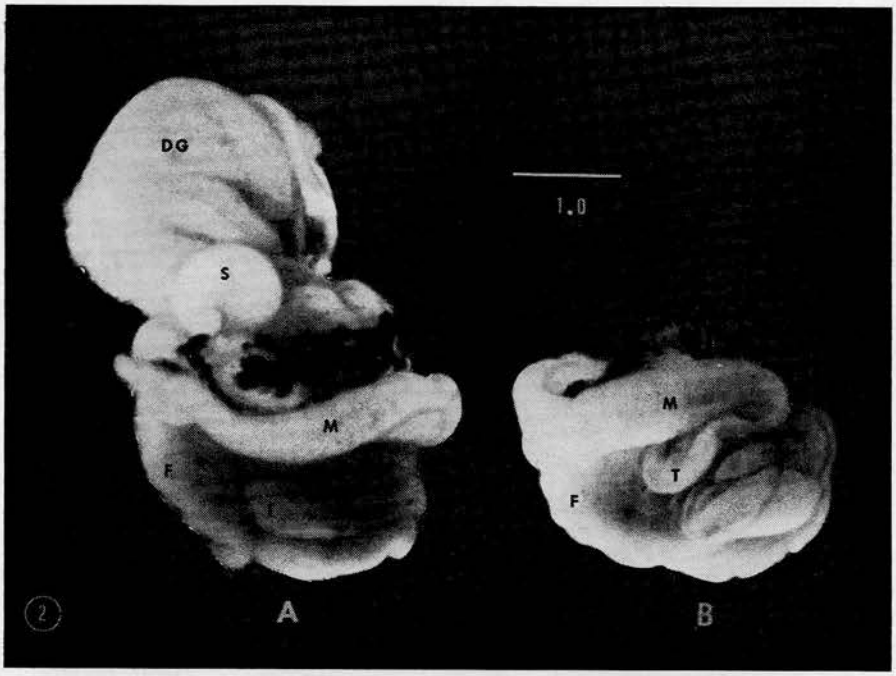
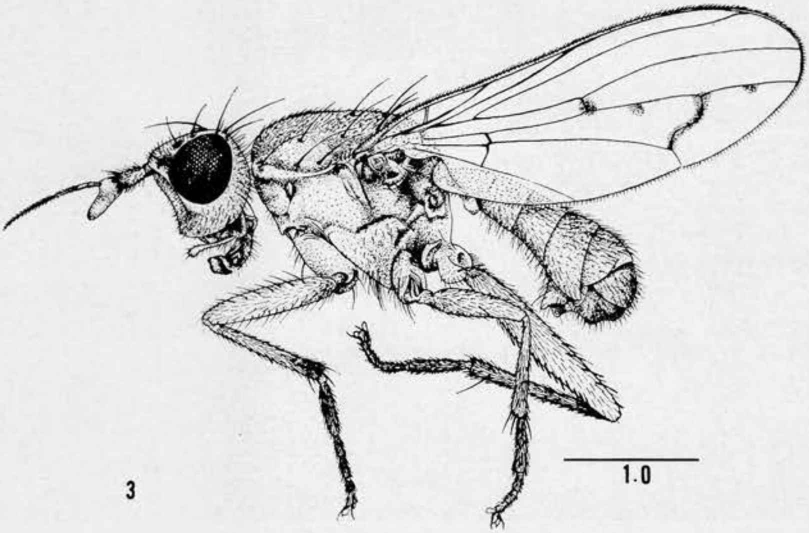


Fig. 1 : Habitat of *K. unipunctata* (MACQUART), Fuente de Cela, Tijola, Almeria Province, Spain (Collector : J. W. STEPHENSON). Fig. 2 : *Lymnaea peregra* (MÜLLER); A, entire soft parts removed from shell; B, soft parts (of another individual of the same size) characteristically left uneaten by larvae of *K. unipunctata* (MACQUART). DG-OT digestive gland and ovotestis; F, foot; M, mantle; T, tentacle.



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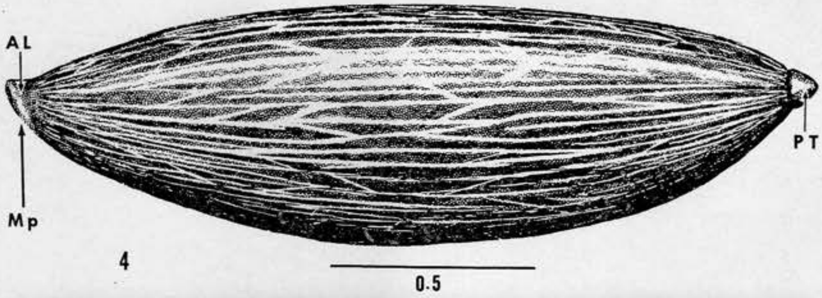

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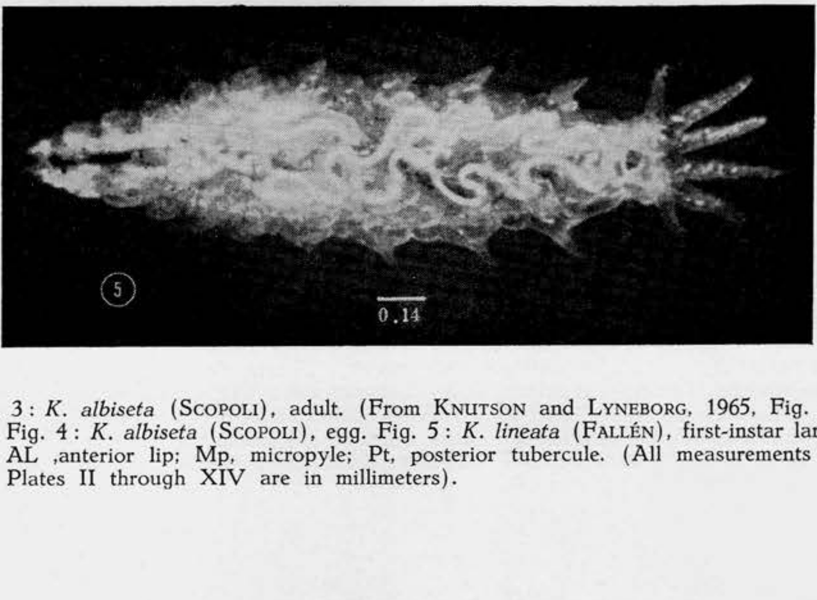

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Fig. 3 : *K. albiseta* (SCOPOLI), adult. (From KNUTSON and LYNEBORG, 1965, Fig. 4). Fig. 4 : *K. albiseta* (SCOPOLI), egg. Fig. 5 : *K. lineata* (FALLÉN), first-instar larva. AL ,anterior lip; Mp, micropyle; Pt, posterior tubercule. (All measurements on Plates II through XIV are in millimeters).

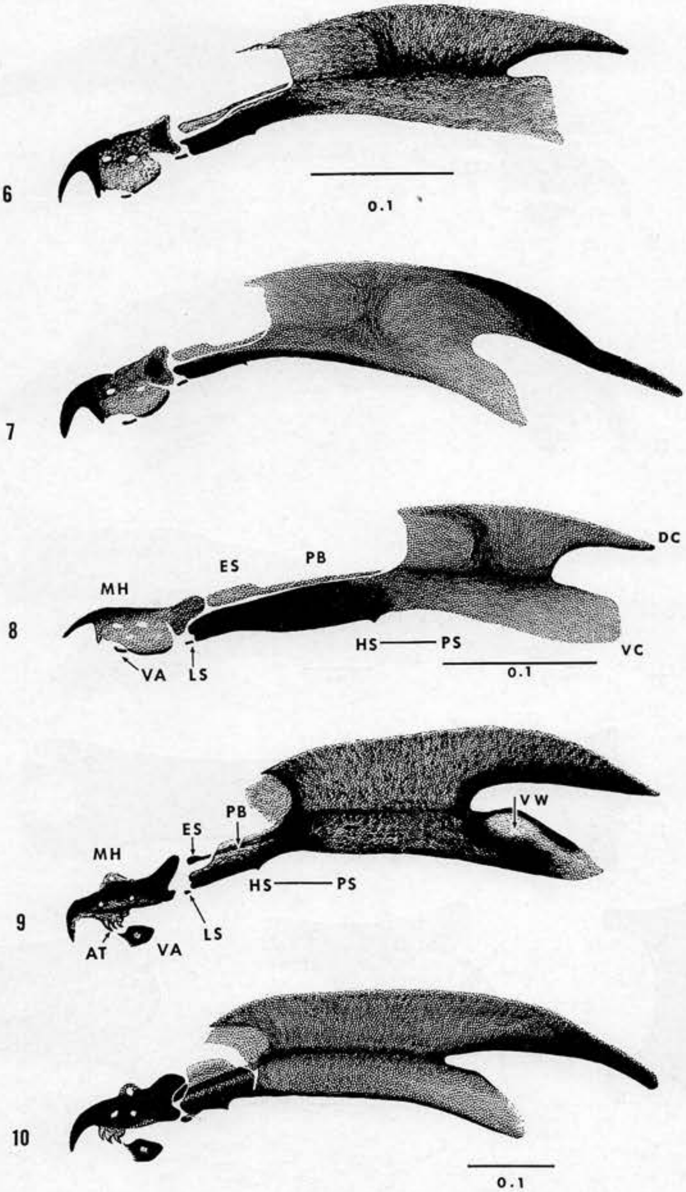


Fig. 6-10. — Cephalopharyngeal skeletons. Fig. 6 : *K. albiseta* (Scopoli), first instar. Fig. 7 : *K. unipunctata* (Macquart), first instar. Fig 8 : *K. lineata* (Fallén), first instar. Fig. 9 : *K. albiseta* (Scopoli), second instar. Fig. 10 : *K. unipunctata* (Macquart), second instar. AT, accessory teeth; DC, dorsal cornu; ES, epistomal sclerite; HS-PS, fused hypostomal and pharyngeal sclerites; LS, ligulate sclerite; MH, mouthhook; PB, parastomal bar; VA, ventral arch; VC, ventral cornu; VW, ventral window.

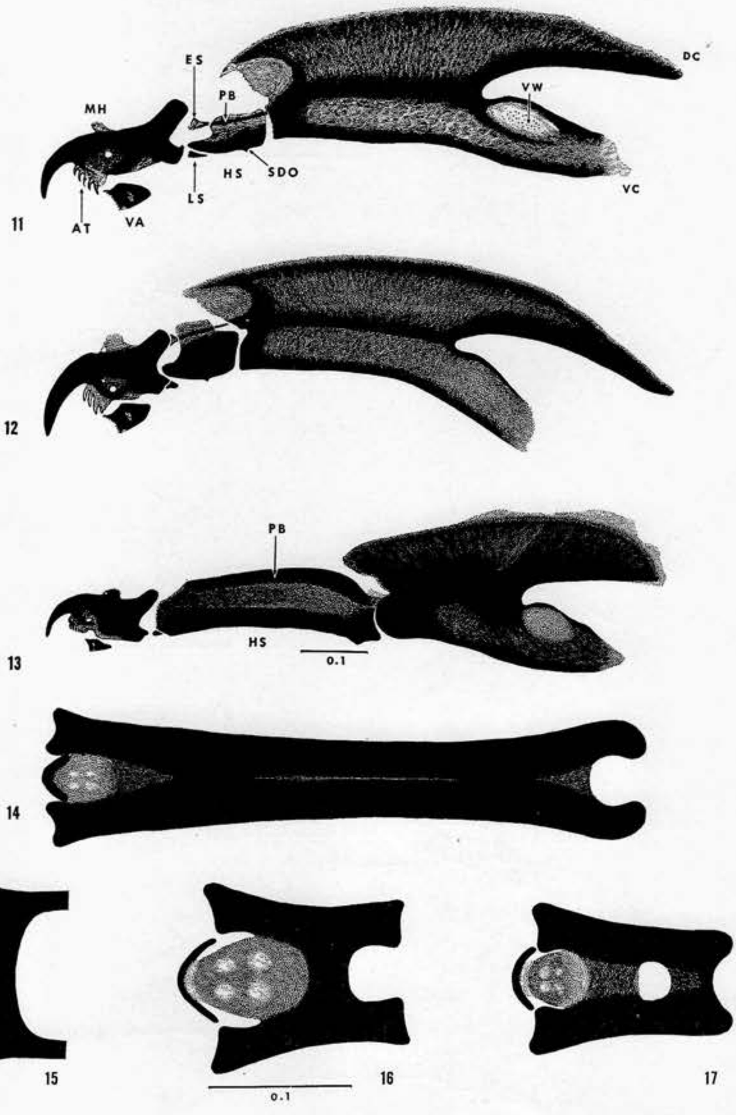


Fig. 11-17. — Fig. 11 : *K. albiseta* (SCOPOLI), third instar, cephalopharyngeal skeleton. Fig. 12 : *K. unipunctata* (MACQUART), third instar, cephalopharyngeal skeleton. Fig. 13 : *K. lineata* (FALLÉN), third instar, cephalopharyngeal skeleton. Fig. 14 : *K. lineata* (FALLÉN), third instar, ligulate and hypostomal sclerites. Fig. 15 : *K. albiseta* (SCOPOLI), third instar, epistomal sclerite. Fig. 16 : *K. albiseta* (SCOPOLI), third instar, ligulate and hypostomal sclerites. Fig. 17 : *K. unipunctata* (MACQUART), third instar, ligulate and hypostomal sclerites. AT, accessory teeth; DC, dorsal cornu; ES, epistomal sclerite; HS, hypostomal sclerite; LS, ligulate sclerite; MH, mouthhook; PS, pharyngeal sclerite; SDO, salivary duct opening; VA, ventral arch; VC, ventral cornu; VW, ventral window.

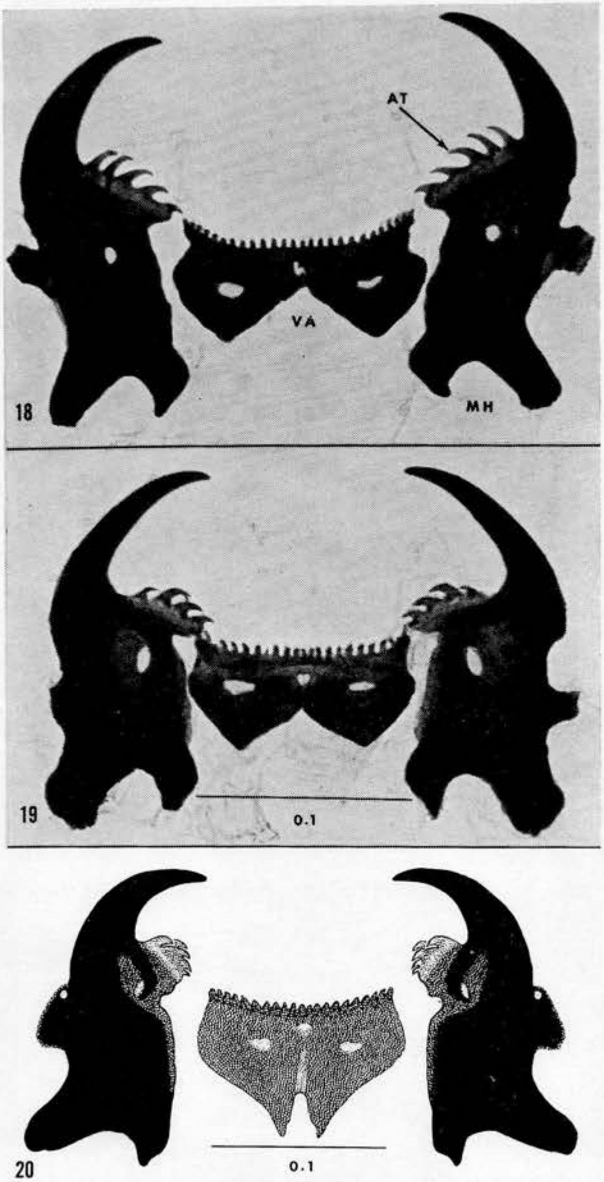


Fig. 18-20. — Mouthhooks and ventral arch, third instar. Fig. 18 : *K. albiseta* (Scopoli). Fig. 19 : *K. corcyrensis* Verbeke. Fig. 20 : *K. lineata* (Fallén). AT, accessory teeth; MH, mouthhook; VA, ventral arch.

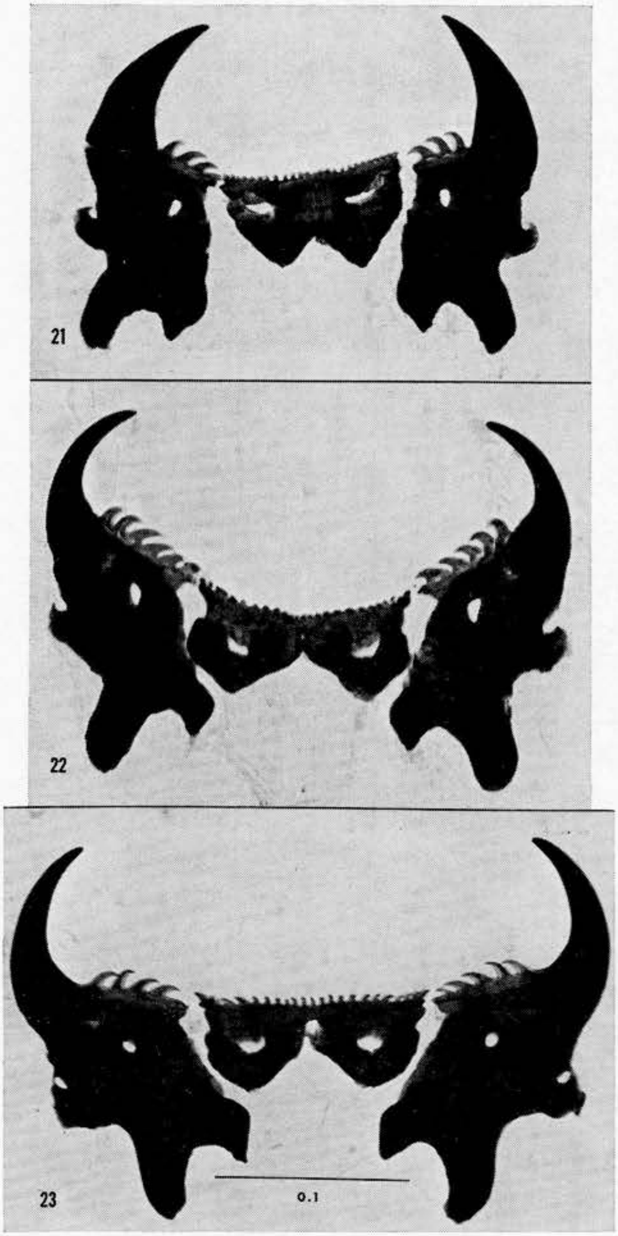


Fig. 21-23. — Mouthhooks and ventral arch, third instar. Fig. 21 : *K. unipunctata* (Macquart). Fig. 22 : *K. turcestanica* (Hendel). Fig. 23 : *K. trifaria* (Loew).

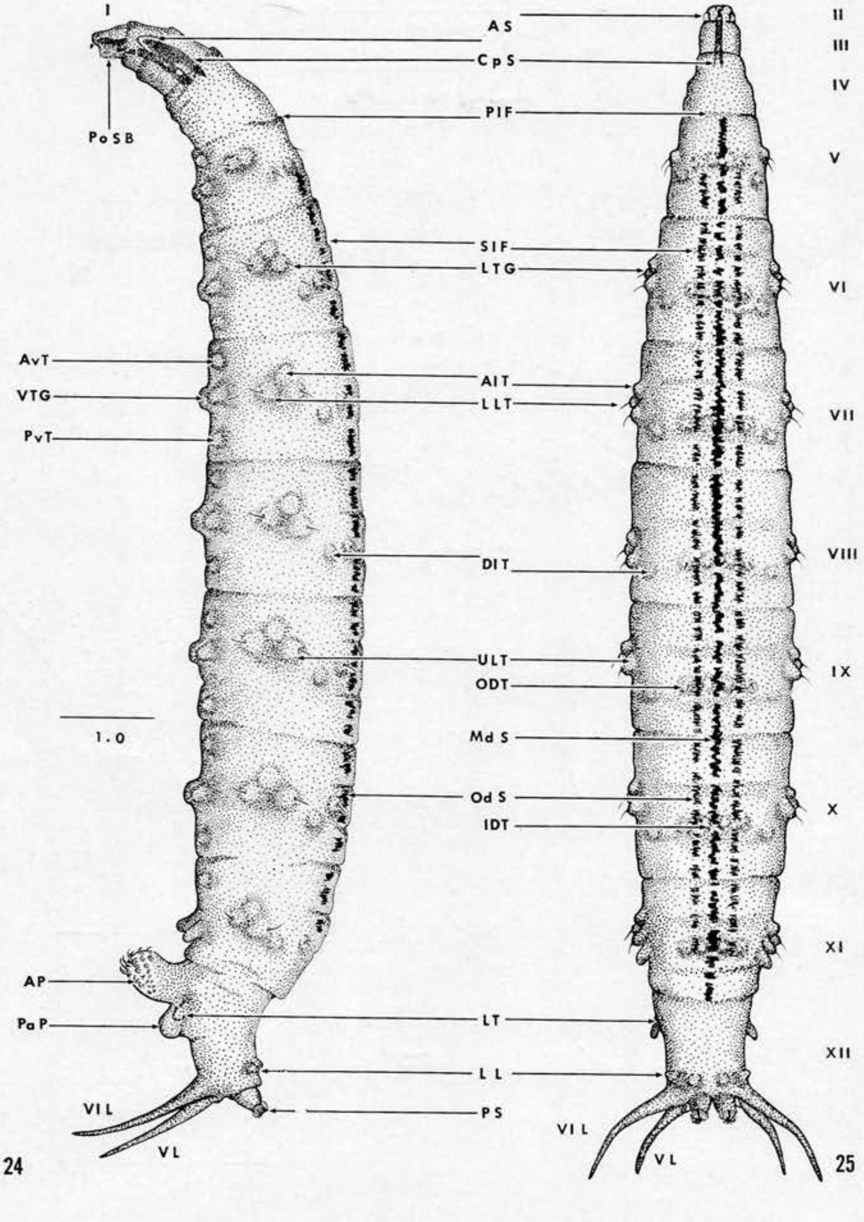
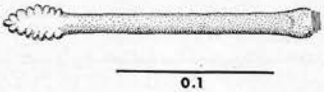


Fig. 24-25. — *K. turcestanica* (HENDEL), third-instar larva. Fig. 24 : lateral. Fig. 25 : dorsal. Alt, anterolateral tubercle; AP, anal proleg; AS, anterior spiracle; AvT, anteroventral tubercle; CpS cephalopharyngeal skeleton; DLT, dorsolateral tubercle; IDT, inner dorsal tubercle; LL, lateral lobe; LLT, lower tubercle; LT, lateral tubercle; LTG, lateral tubercle group; MdS, middorsal stripe; OdS, outer dorsal stripe; ODT, outer dorsal tubercle; PaP, peri-anal pad; PIF, primary integumentary fold; PoSB, post-oral spine band; PS, posterior spiracle; PvT, postero-ventral tubercle; SIF, secondary integumentary fold; ULT, upper lateral tubercle; VL, ventral lobe; VIL, ventrolateral lobe; VTG, ventral tubercle group; I-XII, segments.



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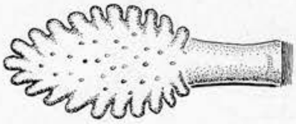

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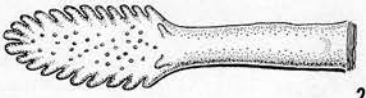

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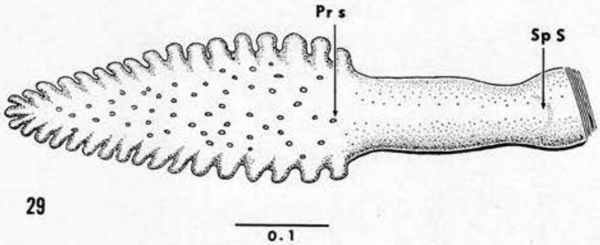

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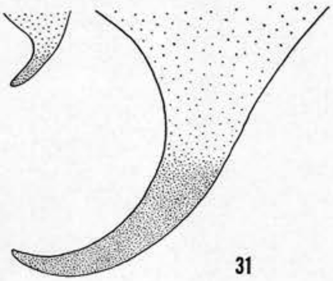

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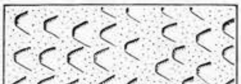

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Fig. 26 : *K. albiseta* (Scopoli), second instar, anterior spiracle. Fig. 27 : *K. trifaria* (Loew), third instar, anterior spiracle. Fig. 28 : *K. unipunctata* (Macquart), third instar, anterior spiracle. Fig. 29 : *K. turcestanica* (Hendel), third instar, anterior spiracle. Fig. 30 : *K. unipunctata* (Macquart), third instar, interspiracular process or « float hair ». Fig. 31 : *K. albiseta* (Scopoli), second instar; hooks on anal proleg. Fig. 32 : *K. albiseta* (Scopoli), second instar, integument. PrS, prismatic spot; SpS, spiracular scar.

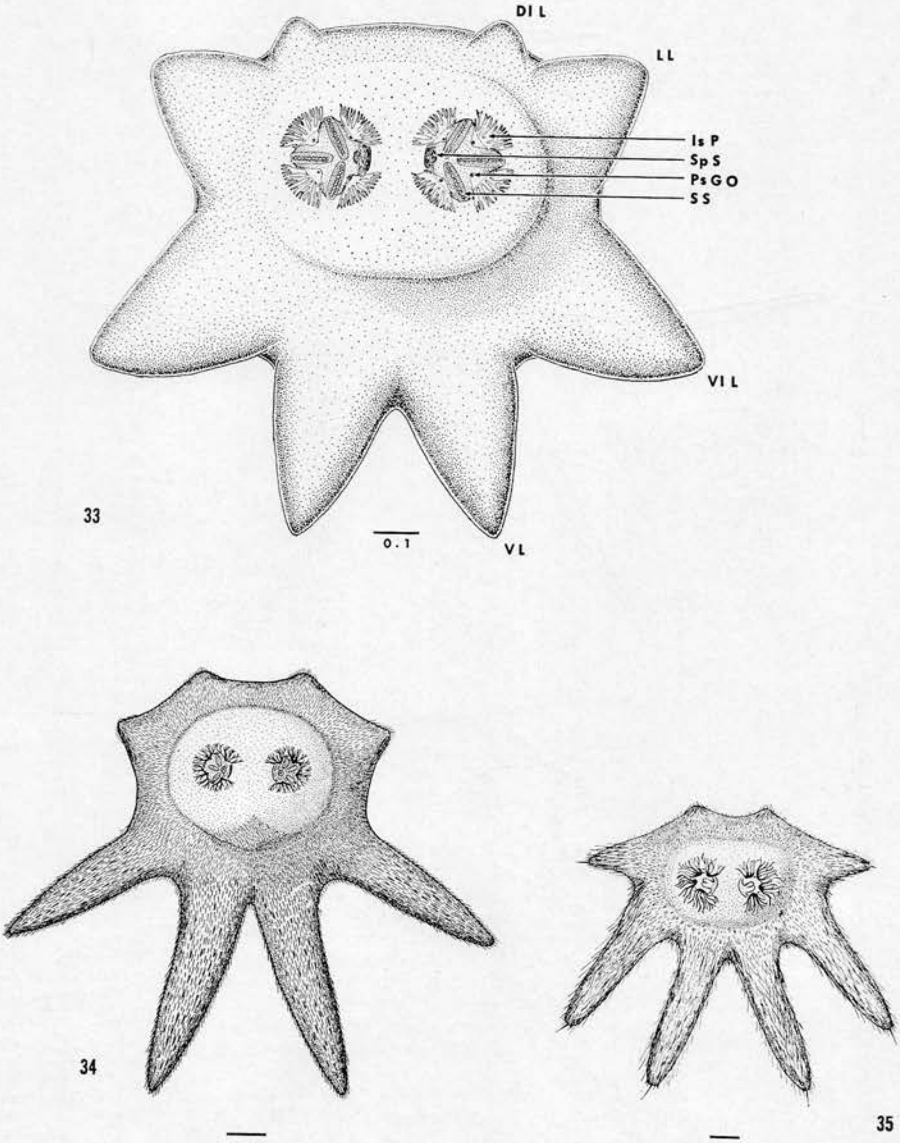

Fig. 33-35. — Posterior spiracular discs. Fig. 33 : *K. unipunctata* (MACQUART), third instar. Fig. 34 : *K. albiseta* (SCOPOLI), second instar. Fig. 35 : *K. lineata* (FALLÉN), first instar. DIL, dorsolateral lobe; IsP, interspiracular process; LL, lateral lobe; PsGO, perispiracular gland opening; SpS, spiracular scar; SS, spiracular slit; VL, ventral lobe; VIL, ventrolateral lobe.

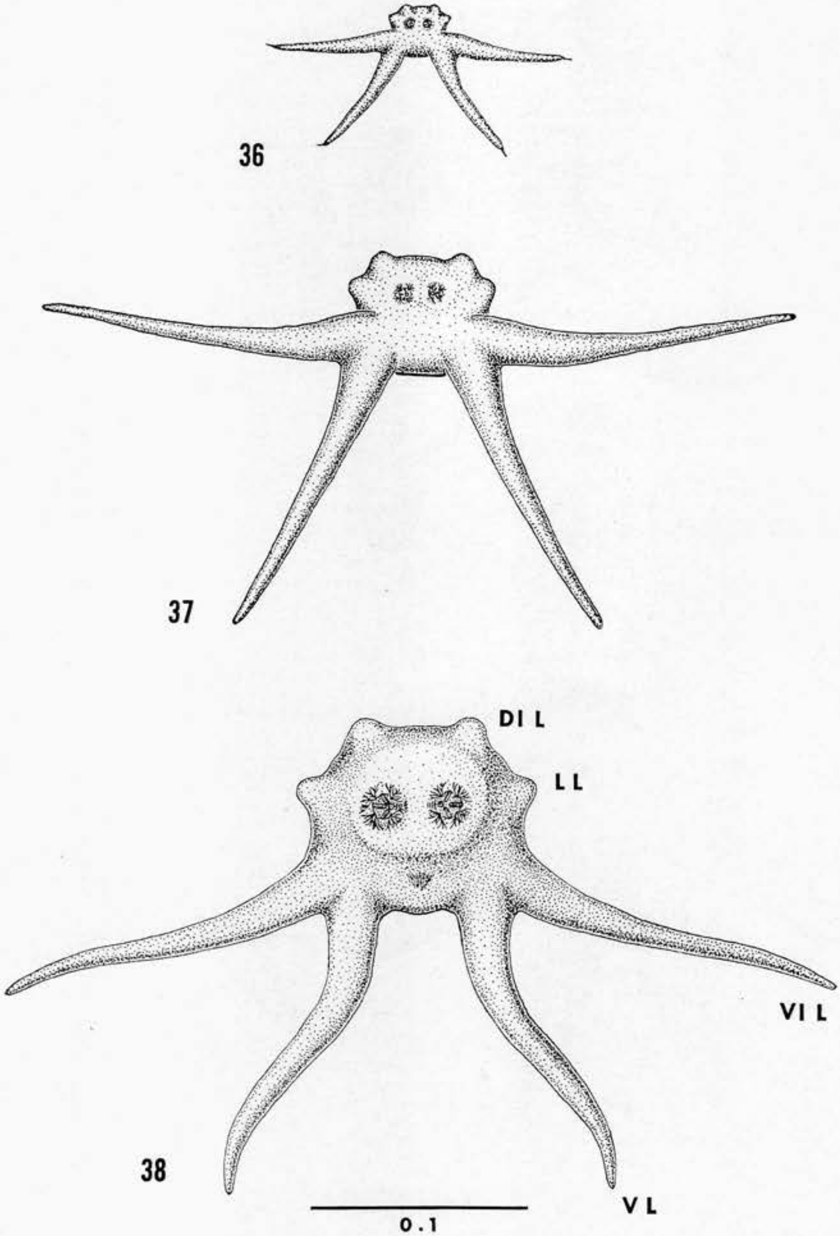

Fig. 36-38. — *K. trifaria* (LOEW), posterior spiracular disc. Fig. 36, first instar. Fig. 37 : second instar. Fig. 38 : third instar. DIL, dorsolateral lobe; LL, lateral lobe; VIL, ventrolateral lobe; VL, ventral lobe.

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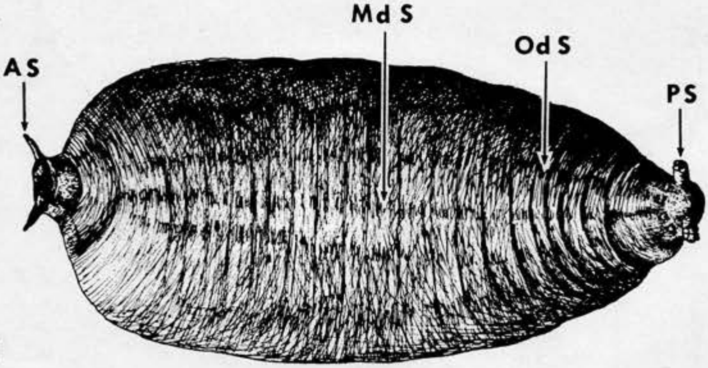

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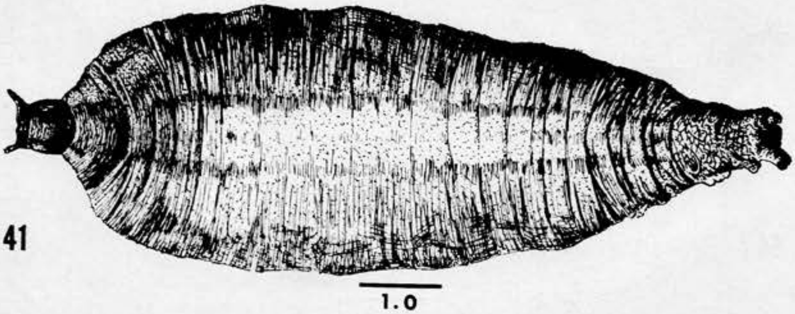

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Fig. 39-41. — Puparia, dorsal. Fig. 39 : *K. unipunctata* (MACQUART). Fig. 40 : *K. albiseta* (SCOPOLI). Fig. 41 : *K. corcyrensis* VERBEKE. AS, anterior spiracle; LV, lobe vestige; MdS, middorsal stripe; OdS, outer dorsal stripe; PS, posterior spiracle.

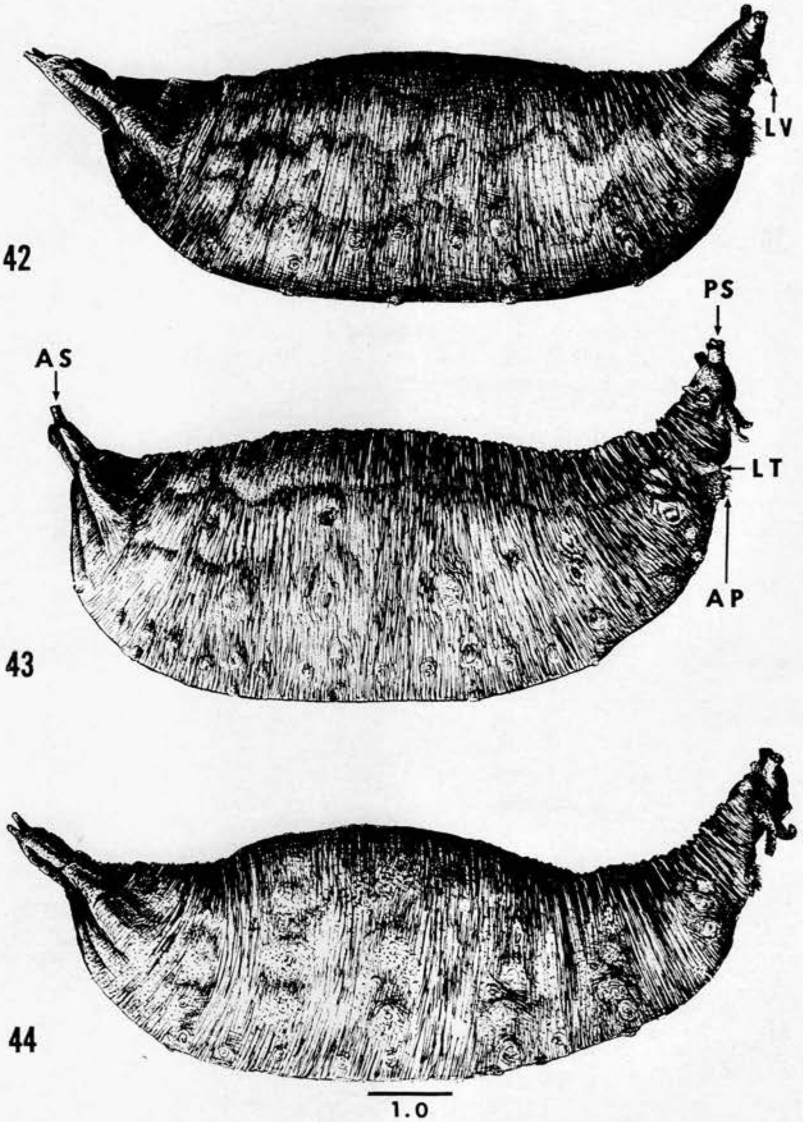
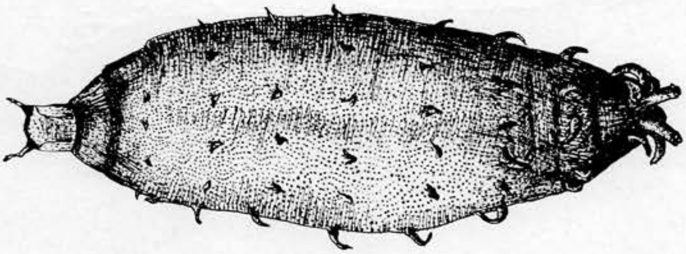


Fig. 42-44. — Puparia, lateral. Fig. 42 : *K. unipunctata* (MACQUART). Fig. 43 : *K. albiseta* (SCOPOLI). Fig. 44 : *K. corcyrensis* VERBEKE. AP, anal proleg; AS, anterior spiracle; LT, lateral tubercle; LV, lobe vestige; PS, posterior spiracle.



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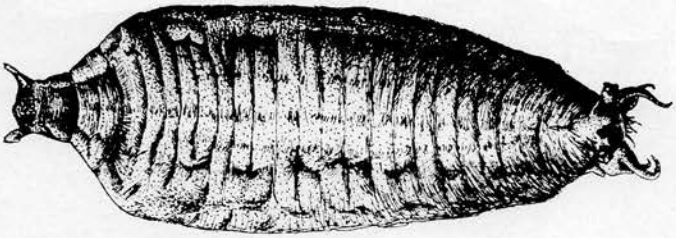

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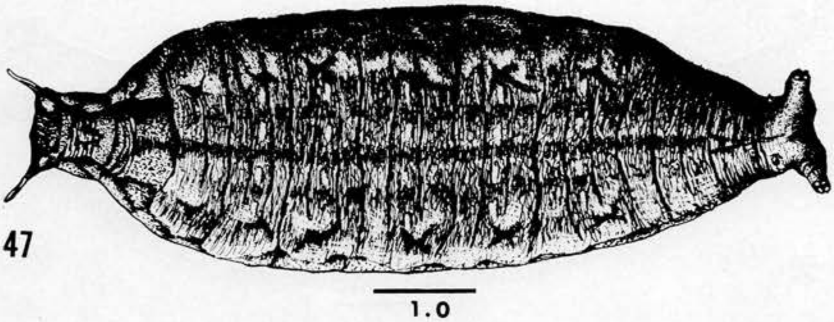

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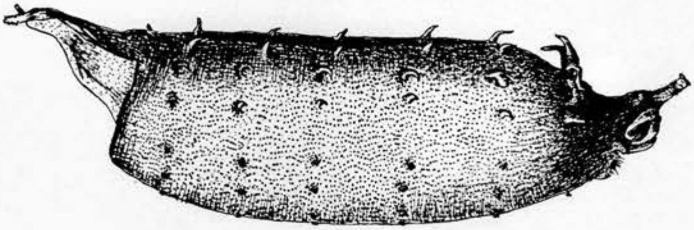
Fig. 45-47. — Puparia, dorsal. Fig. 45 : *K. lineata* (FALLÉN). Fig. 46 : *K. trifaria* (LOEW). Fig. 47 : *K. turcestanica* (HENDEL).



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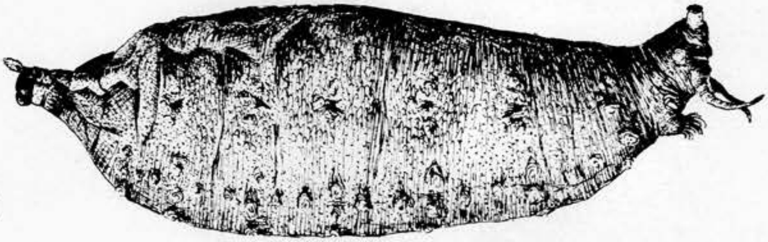

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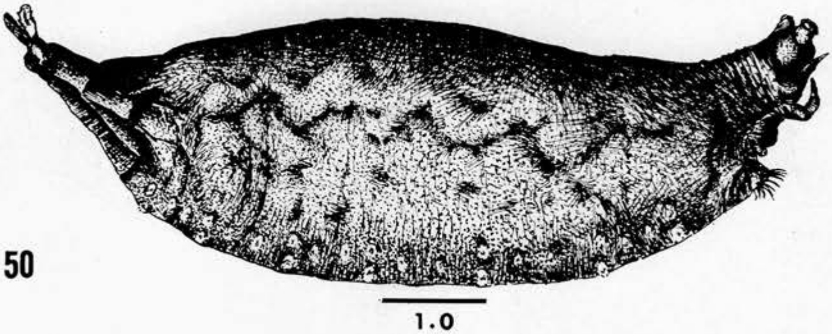

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Fig. 48-50. — Puparia, lateral. Fig. 48 : *K. lineata* (FALLÉN). Fig. 49 : *K. trifaria* (LOEW). Fig. 50 : *K. turcestanica* (HENDEL).

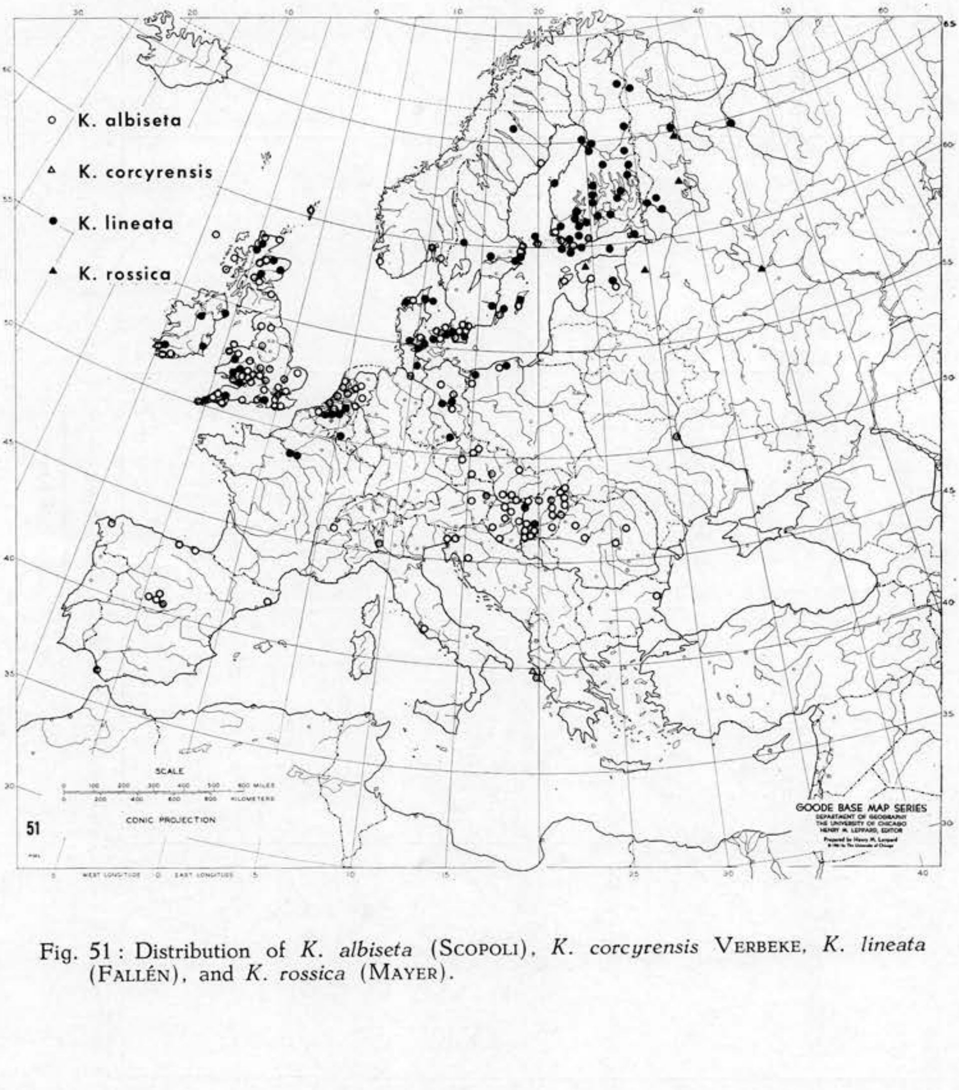

Fig. 51 : Distribution of *K. albiseta* (SCOPOLI), *K. corcyrensis* VERBEKE, *K. lineata* (FALLÉN), and *K. rossica* (MAYER).

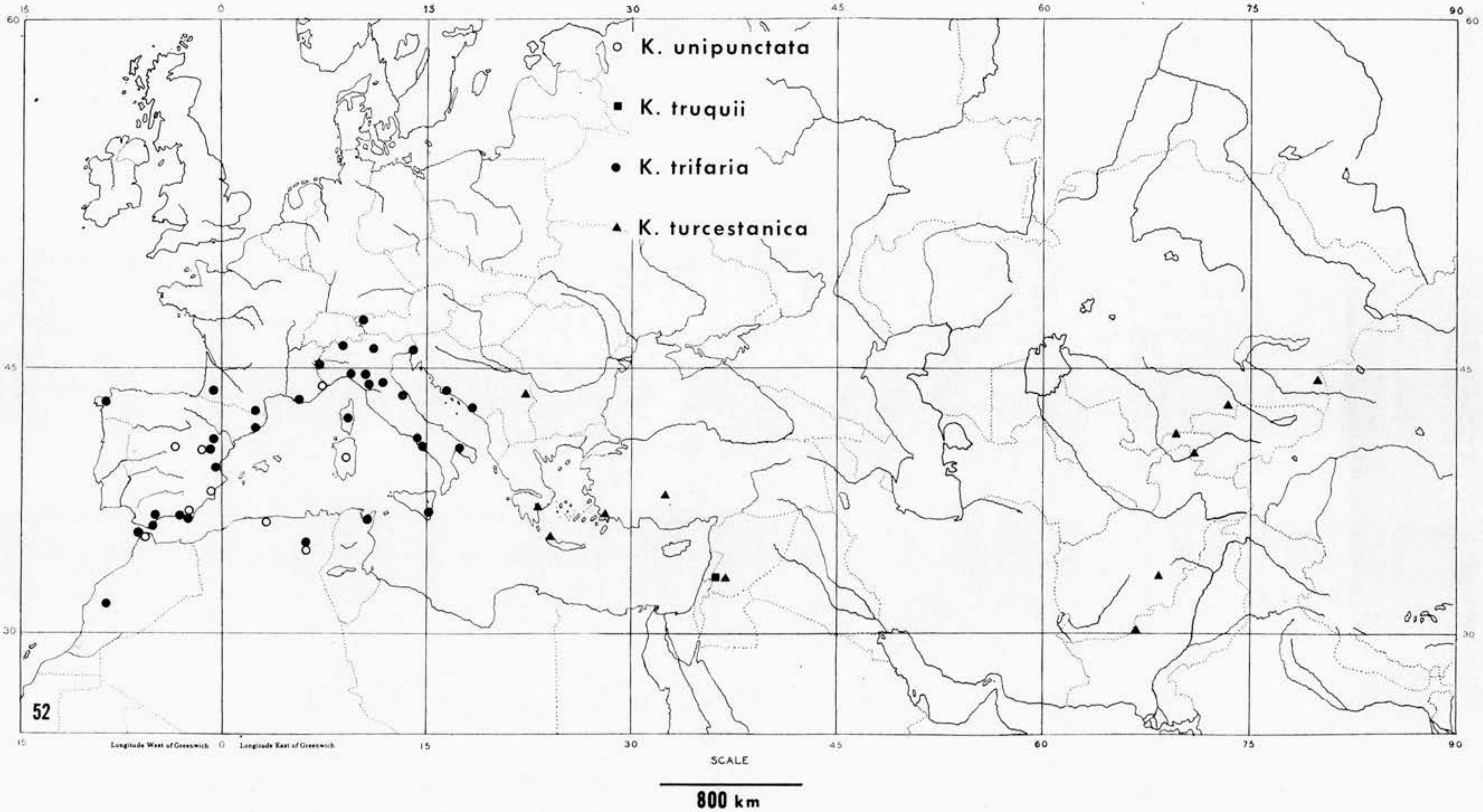

Fig. 52: Distribution of *K. unipunctata* (MAQCUART), *K. truquii* (RONDANI), *K. trifaria* (LOEW), and *K. turcestanica* (HENDEL).

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