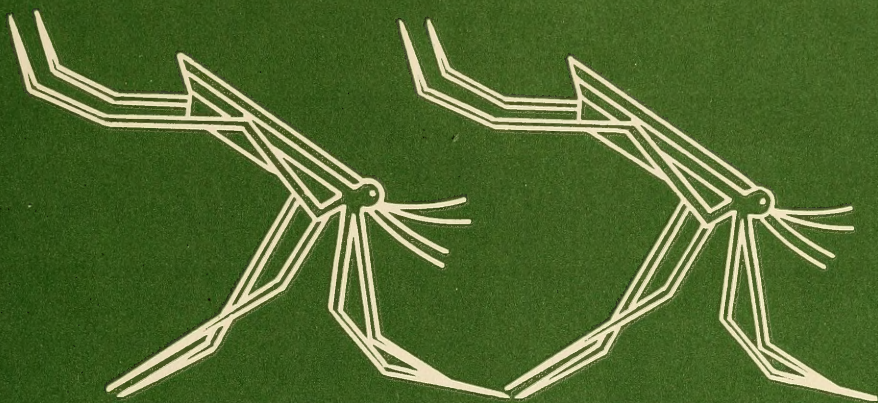




A.V. MASLOV

**BLOOD-SUCKING
MOSQUITOES OF THE
SUBTRIBE CULISETINA
(DIPTERA, CULICIDAE)
IN WORLD FAUNA**

Siberians have given the name "gnus" to the blood-sucking dipterous insects which attack man and domestic animals. These dipterans affect human health and animal behavior. Productivity at work sites also suffers due to these insects. The full impact of these pests has not been adequately studied but available data indicate significant reduction in output of labor exposed to annoying blood-sucking mosquitoes. Unfortunately, the adverse behavior of mosquitoes is not restricted to blood-sucking; many of them are of major economic importance as vectors of diseases affecting domestic animals and man.

Culisetina mosquitoes are interesting in other ways too. A detailed study of the available material has shown that Culisetina mosquitoes have a wide range of variability in all their morphological characters. Great variability of ecological features and the behavior of larvae and specific morphological, ecological and ethological primitiveness of imago and preimaginal stages have been established.

*Blood-sucking Mosquitoes of the Subtribe Culisetina
(Diptera, Culicidae) in World Fauna*

Blood-sucking Mosquitoes of the Subtribe Culisetina (Diptera, Culicidae) in World Fauna

A.V. Maslov

Scientific Editor
RONALD A. WARD



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FOREWORD TO THE ENGLISH-LANGUAGE EDITION

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of P.L. 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

Although written more than twenty years ago, Maslov's treatise remains an indispensable guide to the mosquitoes of the tribe Culisetini. Certain of the species are notorious biting pests of humans and cattle in the more northern areas of North America, Europe and Asia making life intolerable as stressed in the Foreword. Other species are involved in the transmission of various pathogens to humans and domestic animals.

The subtribe Culisetina was proposed by Maslov to encompass our present concept of the tribe Culisetini. Within his tribe Culisetini was a second subtribe, the Mansoniina, which included the genus *Mansonia* (now the genera *Mansonia* and *Coquillettidia*). The Culisetina included the genera *Culiseta*, *Austrotheobaldia*, *Theomyia* and *Allotheobaldia*. Currently, only the genus *Culiseta* is recognized with the other three taxa now considered as subgenera.

Within his Culisetina, Maslov recognized thirty-two species and twelve subspecies. During the intervening years, there have been a number of changes in the status of certain of the species and subspecies treated by him. Those names which have undergone change include:

1. *Culiseta* (*Culiseta*) *annulata subochrea* (Edwards)—elevated to species.
2. *Culiseta* (*Culiseta*) *kanayamensis* Yamada—synonymy with *Cs. bergrothi*.
3. *Culiseta* (*Culicella*) *morsitans dyari* (Coquillett)—synonymy with *Cs. morsitans*.

4. *Culiseta (Culicella) silvestris minnesotae* Barr—elevated to species.
5. *Culiseta (Culicella) silvestris ochroptera* Peus—elevated to species.
6. *Culiseta (Culicella) silvestris* (Shinagarev)—considered *Nomina*

Dubia.

7–11. *Culiseta (Neotheobaldia) drummondi* Dobrotworsky, *otwayensis* (Dobrotworsky), *sylvanensis* (Dobrotworsky), *victoriensis* (Dobrotworsky) and *weindorferi* (Edwards)—transferred to subgenus *Culicella*.

Four additional species of *Culiseta* have been described since 1967. These include:

1. *Culiseta* (subgenus uncertain) *arenivaga* Marks, 1968—Australia.
2. *Culiseta (Climacura) marchettei* Garcia, Jeffery and Rudnick, 1969—Malaysia.
3. *Culiseta (Climacura) novaezealandiae* Pillai, 1966—New Zealand.
4. *Culiseta (Culiseta) megaloba* Luh, Chao and Heu, 1974—China.

In general, the morphological terminology used by Maslov has been retained. One notable exception has been to change the wording of hairs and setae from the original text to only setae to conform with present usage. Editorial changes to the text have been indicated with brackets []. Some of these are corrections of omissions while others may show changes in nomenclature.

The availability of this translation should stimulate research on a rather neglected group of mosquitoes, not only within North America, but elsewhere.

March 15, 1988

RONALD A. WARD
Walter Reed Biosystematics Project
Museum Support Center
Smithsonian Institution
Washington, D.C.

FOREWORD

3 Siberians have given the name "gnus" to the blood-sucking dipterous insects which attack man and domestic animals. During the summer in many regions of Siberia and the Far East, especially in forest and marshy areas, many thousands of winged blood-sucking insects attack man, pierce his skin with their needle-like mouth parts and annoy him with their bites. Even if one insect is driven away, one hundred or one thousand more replace it. At no time during a summer day can man be free of this pest. Domestic and wild animals are also annoyed and attacked by these insects.

These dipterans affect human health and animal behavior. Productivity at work sites also suffers due to these insects. The full impact of these pests has not been adequately studied but available data indicate significant reduction in output of labor exposed to annoying blood-sucking mosquitoes. According to the data collected by Maslov and Shamrai (1955), labor productivity of the Eleventh Forest-cutting Brigade in the Vyazemsk district of Khabarovsk region averaged 88% in the summer of 1953, when there was no protection from blood-sucking mosquitoes. Productivity rose to 110% in the same brigade when dimethylphthalate was used as a repellent. Similar data are available for the Arkhangelsk region (Kalmykov, 1955) and the Karelian Autonomous Soviet Socialist Republic (Lutta, 1956).

That gnus also affect animal productivity is certain. According to data collected from the Far Eastern Institute of Agriculture (I.P. Rykovskii, unpublished work), average milk yield greatly decreased in the summer on many collective farms of the Vyazemsk district. Cattle breeders were convinced that this was due to the presence of many dipterous blood-sucking insects, especially mosquitoes and gadflies. A special survey was conducted by the author in the summer of 1961 on one of the large state farms of the Khabarovsk region. The results showed that the average daily yield of milk per cow in a herd protected from gnus was 12.1 ± 0.18 liters ($n = 132$) in 20 days. At the same time, the yield per cow in an unprotected herd, under analogous conditions, was only 4.9 ± 0.12 liters ($n = 89$). These values reflect the effect of mosquito bites. Similar phenomena have been observed in other districts of the Khabarovsk region.

The relative importance of different groups of dipterous blood-sucking insects of the gnus type is not uniform in different topographic and geographic zones of the USSR, or the world as a whole, nor in different years and even in different seasons of the same year in the same region. Among blood-sucking mosquitoes which attack man in the northern regions of Europe, Asia and North America, especially in the spring and early summer, those of the genus *Culiseta* (*C. alaskaensis* Ludl., *C. bergrothi* Edw., *C. impatiens* Wlk., and others) are economically important; attacks by Culisetina mosquitoes are sometimes reported even in temperate regions.

- 4 Unfortunately, the adverse behavior of mosquitoes is not restricted to blood-sucking; many of them are of major economic importance as vectors of diseases affecting domestic animals and man.

While some groups have been thoroughly studied (*Anopheles* in connection with malaria; *Anopheles* and some species of *Culex* and *Aedes* in connection with yellow fever; these groups of mosquitoes in connection with wuchereriosis [Bancroftian filariasis] and autumn [Japanese] encephalitis and others), there are quite a few for which epidemiological data are either very scanty or totally lacking. These include Culisetina, which are widely distributed almost everywhere in the world. These are relatively less numerous and less bothersome than other mosquitoes in many regions. Therefore, the biology of Culisetina has not been vigorously investigated although mosquitoes now placed in this group have been known since the time of Schrank who described *Culex annulatus*, representing the type genus and subgenus *Culiseta* Felt (Schrank, 1776).

In the 200 years since Schrank's research, quite a bit of information has accumulated in the literature on Culisetina mosquitoes. However, reference to these mosquitoes was comparatively rare until the beginning of the 20th century.

The early 20th century, when Culisetina mosquitoes were grouped in an independent genus (Neveu-Lemaire, 1902; Felt, 1904), represented a turning point at which innumerable research papers on the ecology, biology, morphology and fauna and systematics of this genus appeared in world literature.

Interest in Culisetina mosquitoes grew rapidly after references appeared in literature about the very severe sickness caused by the bites of species of this genus and even more so after some species of *Culiseta* were suspected of spreading infectious diseases among man and domestic animals. Data are limited on epidemiological transmission by Culisetina mosquitoes. In the United States of America, *Culiseta melanura* Coq. has been recognized as the main vec-

tor of eastern equine encephalomyelitis (EEE)* among birds; it has also been incriminated as an additional carrier of western equine encephalomyelitis (WEE). There are two other American species, *C. inornata* Will. and *C. incidens* Thoms., which are economically important in the transmission of these infections and St. Louis encephalitis (SLE)**. The possible transmission of autumn (Japanese) encephalitis virus by *C. inornata* (Reeves and Hammon, 1946) has been experimentally demonstrated; a new virus of the "Bunyamvera" group has recently been isolated from the mosquitoes of the same species in northern Utah (Holden and Hess, 1959), while three strains of group A viruses have been isolated from New Zealand *C. tonnoiri* (also *Culex pervigilans*); one of these strains is genetically related to Sindbis (MKM-39) virus and western encephalomyelitis (WEE) (Ross, et al., 1963). For the European members of Culisetina group, data are available on the economic importance of *Allotheobaldia longiareolata* Macq. (Malta fever, avian influenza, and West Nile encephalitis) (Hurlbut, 1956; Séguy, 1924) and of *Culiseta annulata annulata* Schr. (avian influenza and fowl pox) (Bos, 1934; Séguy, 1925). In the USSR, Culisetina mosquitoes

5 have remained little investigated. Only very recently has the author noticed the spontaneous infection of *Culiseta bergrothi* mosquitoes by microfilariae in central Amur and experimentally demonstrated the persistence of the microfilaria *Dirofilaria immitis* Rail and Henry in the midguts of these mosquitoes infected on dogs.

Culisetina mosquitoes are interesting in other ways too. A detailed study of the available material has shown that Culisetina mosquitoes have a wide range of variability in all their morphological characters (Maslov, 1952, 1957a, 1957b and 1962a). Great variability of ecological features and the behavior of larvae and specific morphological, ecological and ethological primitiveness of imago and preimaginal stages have been established in *C. bergrothi* and some other species (Maslov, 1952, 1955a, 1957b, 1960a, 1961e and 1963). Therefore, Culisetina mosquitoes are a very convenient model for experimental study of such common biological questions as patterns of variation, responses of the organism to external environmental conditions, aspects of metamorphosis, intraspecific relations, and so on (Maslov, 1952, 1955, 1957a, 1957b, 1960a, 1960b, 1961a–1961e, 1962a and 1963).

Since it is impossible to discuss in this limited volume all the

*Works of various authors (Chamberlain, et al., 1958; Hayes, et al., 1960; Hess and Holden, 1958; Holden, et al., 1954; Kissling, 1958; and others).

**See Eklund, 1954; Hammon and Reeves, 1943a, 1943b; Hammon, et al., 1943 and 1945; Reeves and Hammon, 1946; and others.

interesting aspects of this subject, the author has restricted himself mainly to practical systematics (review of the members of the subtribe Culisetina throughout the world). However, he considers it essential that the first part of the monograph be enlarged by including therein data on variations in morphological characters. Unfortunately, within this limited scope, it has not been possible to examine the ecology, development and behavior of the members of Culisetina. These have received an extremely cursory description with each species.

The author expresses his sincere gratitude to his many associates who aided him in the collection of specimens and literature, in field and experimental investigations, in laboratory research and with other supportive assistance.

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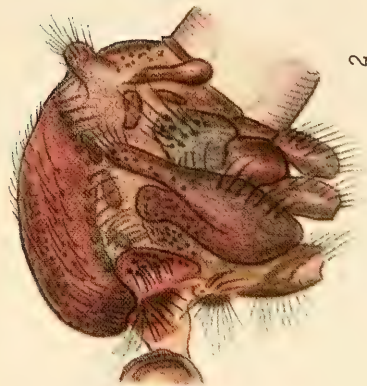
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4. Genus *Allotheobaldia* Brol.

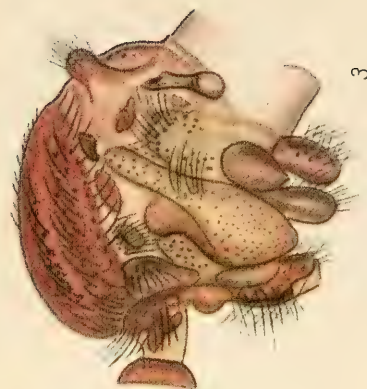
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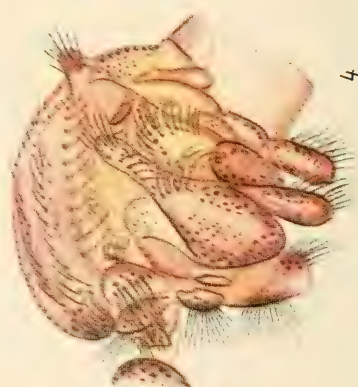
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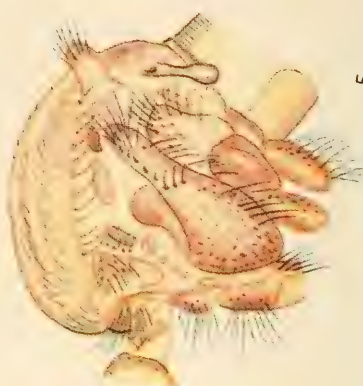
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3



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5



6

Fig. 1. Types 1-6 of thoracic coloration.

INTRODUCTION

MORPHOLOGY OF ADULT MOSQUITOES

8 *Size and color.* Tribe Culisetina includes large or medium size mosquitoes, only slightly smaller than *Psorophora*, *Toxorhynchites* (syn. *Megarhinus*), *Opifex* and some other genera found outside the Palearctic region. We note the unreliability of measurements of mosquitoes determined from preserved museum specimens. In insects with membranous intersegmental regions, the abdomen could be highly distended making it impossible to obtain correct measurements. Even in fresh specimens, the abdominal dimensions vary significantly depending on the intake of food and the distension of the intestine and on the varied development of the fat body and other organs.

Therefore, to describe the range of variation of linear measurements of mosquitoes, only those characters should be selected which remain unaltered throughout the life span of the adult mosquito. Such features include organs with heavily sclerotized integument like the proboscis, measured from the base to the apex including the labial palps; the femora, tibiae and basal tarsal segments measured along their anterior or posterior margins, that is, from the place of union with the preceding segment to the apex (without spines); finally, the wing length measured not from the point of its union with the mesothorax but from the distinctly visible humeral vein to the apex of the wing; and the maximum wing width without scales. Maslov's (1963) investigations concluded that proboscis length was the most useful character. The body of adult mosquitoes is heavily sclerotized by a chitinous integument with innumerable scales, setae,* and spines of various sizes (Fig. 2). In the cuticle of adult Culisetina mosquitoes only melanin is present; this substance determines the color of the integument, dark scales and setae and purine pigments in white scales. On the whole, the color and pattern of the wings and legs of Culisetina are not so much due to the pigmentation of the integu-

*Throughout the original text, hairs and setae are used. For uniformity, the terms seta and setae are applied to cuticular projections which arise from a basal alveolus [Editor].

ment itself (brown, dark brown and even black in a vast majority of specimens), as to the nature and arrangement of the scales densely covering the abdomen, legs and wing veins. Based on a comparison of the data obtained in a study of the coloration of Culisetina, 6 classes of coloration of mosquitoes of this group have been established; they are shown in the form of a variation scale in Fig. 1.

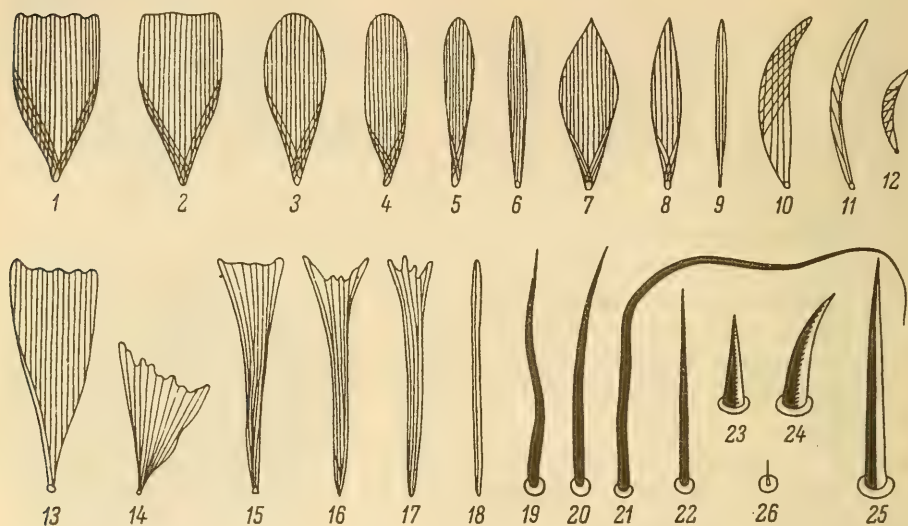


Fig. 2. Types of scales (1-18), and setae (19-26) in adult mosquitoes.

Scales: 1—Broad leafed with wavy margin; 2—same with a smooth margin; 3—same with rounded margin; 4 and 5—narrow leafed; 6—linear; 7—broad lanceolate; 8—narrow lanceolate; 9—acicular; 10—broad crescent-shaped; 11 and 12—narrow crescent-shaped; 13 and 14—irregular broad leafed; 15 to 17—upright furcated and 18—hair-like; setae and spines*; 19—soft, short seta; 20—seta; 21—soft, long seta; 22—seta; 23—upright spines; 24—flexed spine; 25—long spine; 26—microtrichia.

All wing color variations observed in the available material fall within these six types but the body integument usually appears somewhat darker compared to the wing color. This is particularly evident when the wings are covered not with dark scales of a single color, but with a mixture of light (white) and dark scales. Based on an analysis of the quantitative proportions of light and dark scales on

*The structures labeled "spines" (23-26) appear to be setae as they arise from a basal alveolus. By definition a spine is a type of non-articulated, cuticular projection, directly contiguous with the cuticle [Editor].

the wings of all Culisetina mosquitoes under study, variations in this character have been categorized in 6 classes. These are shown in Fig. 3.

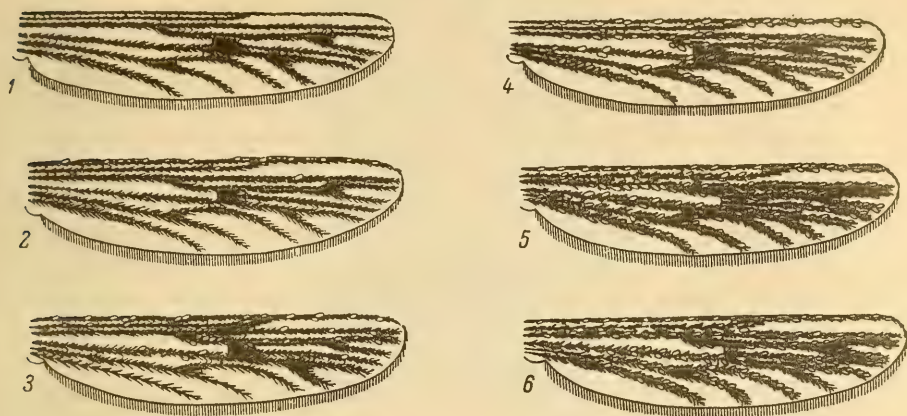


Fig. 3. Classes (1-6) of wing design—distribution of dark and light scales.

The wing pattern is set not only by the extent of light scales arranged on a dark background but by the varying extent of development of spots formed by the accumulation of dark scales on different sections of the wing. In this respect Culisetina mosquitoes are highly diverse as shown in Fig. 4 in the form of variations in scales in six classes.

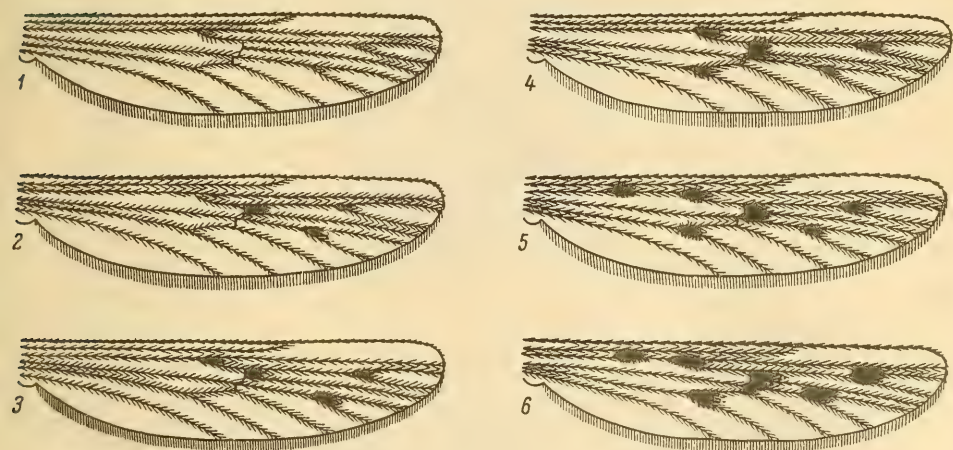


Fig. 4. Classes (1-6) of wing spots.

Head and its appendages. The cranium of most Culisetina mosquitoes is black or blackish brown and is invariably darker than the other body sections. On the top and sides, on the vertex, occiput and genae we find flat, closely adhering scales (Fig. 2, 10–12) with upright furcated scales and setae (Fig. 2, 16, 17 and 20). In many cases, relatively short upright scales are distinctly visible on the occiput; they are elongated anteriorly and gradually narrow into long setae directed forward. Frequently, a specific combination of dark and light scales forms a fairly distinct pattern, particularly evident in *Allotheobaldia longiareolata*. The margins of the eyes in an overwhelming majority of Culisetina are edged with snow-white or silvery, small, narrow, crescent-shaped scales. The frontoclypeal region is usually covered with flat, lanceolate or leaf-like scales with no erect scales but with an admixture of short setae.

The antennae, belonging genetically to the second cephalic segment, consist of 15 segments in both females and males. The first basal segment (scape) is narrow, ring-shaped and barely distinguishable. The second, known as the pedicel or torus, is large, bare and hemispherical with a deep pit at the center where the third segment of the antenna is attached. The particularly well developed torus in the male carries the Johnston's chordotonal organ serving as a sensory and probably sound receptor organ which is evidently very important to swarming mosquitoes (Hayes, 1958; Hubert, 1953; and others). The rest of the antennae, called the flagellum, consists of 13 segments covered with microtrichia, is articulated to the pedicel and is mobile. In females (Fig. 5) each flagellar segment is cylindrical and carries at the base (the first flagellar segment medially) 4–8 moderately long setae, radially disposed.

In males (Fig. 6) the flagellum has a very different, highly typical structure. Each typical segment (Fig. 7) begins with a narrow, weakly sclerotized base and gradually widens towards the center where the highly sclerotized ring, resembling in form a condensed speculum, is distinctly visible; in cross section it is not regularly round but is bilobate. This ring bears very long, radially diverging setae on its broadened, heavily sclerotized part. These setae are numerous on each segment.

The first flagellar segment differs from the others in that its sclerotized ring with setae is placed almost at the very apex and similarly long or slightly shorter setae from a medial ring. It is possible that the first flagellar segment of the antenna represents the fusion of two segments which were originally independent. In that case, the number of antennal segments in the male would be 16 and not 15. In the penultimate, highly elongated segment the sclerotized



Fig. 5. Antenna and maxillary palps in female.



Fig. 6. Male antenna.

ring with setae is present almost at the base, while the rest of the segment is in the form of an extended tube of the ring, densely covered with short setae. The last antennal segment is similarly densely covered with short setae and basally bears 5–10 moderately long setae resembling a rosette on the antennal segments of the female. In addition to these long and short setae, the antennae are covered with tiny crescent-shaped scales.

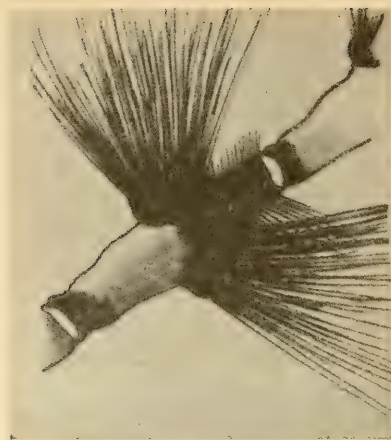


Fig. 7. Separate antennal segment of male.

Mouth parts. The proboscis of Culisetina, as in all mosquitoes of the family Culicidae, represents a rare instance of elongation of mouth parts adapted to blood-sucking (in females). It consists of all the basic parts of the primitive mandibular apparatus in the form of
12 acicular and tubular structures. At rest all of them lie in a sheath (compared with other parts) in a groove of a large labium bearing three segmented paired labial palps and an unpaired glossa at its apex. The soft labium does not take part in blood-sucking but bends when the piercing-sucking mouth parts pierce the skin of the host.

The labrum is not a groove covering the hypopharynx as in other blood-sucking longicorn [nematoceran] dipterans* but is tubular (Martini, 1929-1931; Shvanvich, 1949; Snodgrass, 1944, 1959) with an oblique incision on the free end like that of a syringe needle. The groove of the labrum opens at this free end and the sucked blood enters the pharynx through this duct. The hypopharynx, found under the labrum, is also a small tube with a sharp end through which runs the salivary duct. The paired maxillae and mandibles are very thin, elongated needles with slightly broadened and barbed apices. The barbs on the mandibular apex are hardly distinguishable due to their minute size while they are distinct on the maxillae.

Among the mouth parts, the labrum, labium and hypopharynx
13 are reduced in males. The maxillae and mandibles are wholly or

*Some recent investigators referred to the grooved structure of the labrum, for example, Natvig, 1948.

Table 1. Mandibular palps and maxillary indices in males of some Culicetina

Species	n	0. Class of struc- ture of 2nd and 3rd segments of maxillary palp*	1. Mandibular index, %*		2. Maxillary index, %*		Coefficient of correlation		
			M ± SE	M ± SE	M ± SE	r ₀₁ ± SE _r	r ₀₂ ± SE _r	r ₁₂ ± SE _r	
<i>Culiseta bergrothi</i>	129	3.22 ± 0.08	76.7 ± 0.22	33.7 ± 0.34	+0.803 ± 0.031	+0.809 ± 0.03	+0.426 ± 0.072	r _{0,12} = +0.0955 ± 0.008**, (2) r ₀₁ = +0.862***	
<i>C. alaskaensis indica</i>	34	3.21 ± 0.08	74.2 ± 0.341	26.2 ± 0.33	+0.680 ± 0.092	+0.766 ± 0.071	+0.788 ± 0.065		
<i>C. annulata annulata</i>	85	2.68 ± 0.055	75.5 ± 0.23	24.95 ± 0.21	+0.755 ± 0.043	+0.773 ± 0.044	+0.588 ± 0.071	+0.651 ± 0.068	
<i>C. annulata subochrea</i>	71	2.68 ± 0.075	75.6 ± 0.23	25.6 ± 0.25	+0.772 ± 0.048	+0.786 ± 0.045	+0.588 ± 0.071	+0.651 ± 0.068	
<i>C. silvestris amurensis</i>	30	2.3 ± 0.084	67.0 ± 0.46	10.03 ± 0.29	+0.72 ± 0.088	+0.74 ± 0.083	+0.39 ± 0.154	+0.39 ± 0.154	
<i>C. setivatra</i>	30	2.13 ± 0.062	66.3 ± 0.51	9.07 ± 0.225	+0.38 ± 0.156	+0.21 ± 0.174	+0.377 ± 0.156	+0.377 ± 0.156	
<i>Allothoebaldia longiareolata</i>	102	3.58 ± 0.064	72.9 ± 0.37	31.8 ± 0.32	+0.796 ± 0.036	+0.943 ± 0.011	+0.726 ± 0.047	+0.726 ± 0.047	
							r _{0,12} = +0.487 ± 0.076		

*Numerals 0, 1 and 2 are used to denote the characteristics under correlation (r₀₁ and so on).

**The coefficient of correlation for all three characteristics:

$$r_{0,12} = \sqrt{1 - \frac{1 + 2(r_{01} \times r_{02} \times r_{12}) - r_{01}^2 - r_{02}^2 - r_{12}^2}{1 - r_{12}^2}}$$

***The coefficient of partial correlation (2):

$$r_{01} = \frac{r_{01} - r_{02} \times r_{12}}{\sqrt{(1 - r_{02}^2)(1 - r_{12}^2)}}$$

partly reduced. Having studied this aspect in some members of the family Culicidae, Marshall, Staley and Staley (1935) presented some interesting data on the comparative measurements of the length of maxillae and mandibles in percentage of the length of the proboscis: according to their data, in *Culiseta* mosquitoes, the maxillae of males are marked by maximum relative length compared to other Culicinae. The results of a special study of this character in various members of Culisetina are presented in Table 1. The table shows that the mandibular index (ratio of its length to that of proboscis along with labial palps) is greatest in males and most variable in members of the subgenus *Culiseta* s. str. and in *Allotheobaldia longiareolata*. This index is noticeably low in members of the subgenus *Culicella*. The maxillary indices also vary in roughly the same proportion (Table 1).

Attention should be paid to the structures of the maxillary palps which are often used as taxonomic indices.



13 Fig. 8. Classes (1-5) of the structure of the 2nd and 3rd maxillary palpal segments in males.

In the literature, the number of maxillary palpal segments in males and females has been a very controversial subject. Howard, Dyar and Knab (1913, 1915) referred to 5-segmented palps in males and 4-segmented in females of *Culex pipiens*. Becker (1908) referred to 4-segmented palps in males and females of *Culex pipiens* but 5-segmented palps in males of *A. longiareolata*; Meinert (1886) and Ficalbi (1899) showed 4 and 3 segments for males and females, respectively. Matheson (1929 and 1944) noted that the number of

palpal segments varied from 3 to 5 and reaffirmed this view in both editions of his handbook. Martini (1929–31) reported 5 segments in males of *Anopheles* and 4 in all other Culicidae. Martini (1929–31) noted the complete fusion of the 2nd and 3rd segments of male palps in most Culicini including all species of Culisetina. Due to this fusion their palps appear to be 4-segmented, since they consist of the 1st, 2nd+3rd, 4th and 5th segments. Edwards (1932a) and
 14 many other scientists described the structure of maxillary palps of Culicini males in a similar manner. The fused 2nd+3rd segment was even given a special name: (longes glied), long segment or long joint.

On the contrary, Felt (1904), Snodgrass (1959) and some others found 5-segmented palps in males as well as females of most mosquitoes.

An extensive study of this character conducted by the author for several years revealed a wide variation in this character, at least in Culisetina. Some males were found in which the margin between the 2nd and 3rd palpal segments was absent, but there were others in which each segment was fully developed with a distinct articulation between them. To study the variation of this characteristic in different species of Culisetina, the following categories have been defined (Fig. 8).

1. Boundary between the 2nd and 3rd segments of maxillary palp absent.
2. Boundary between the 2nd and 3rd segments noticeable only from the disposition of setae and scales.
3. Boundary between the 2nd and 3rd segments noticeable in the form of an annular depression of the integument.
4. Boundary between the 2nd and 3rd segments distinct, in the form of a deep annular furrow resembling a joint.
5. Second and 3rd segments distinctly demarcated and joined to each other, mobile.

An examination of the data shown in Table 1 on the variation of the characteristics of 2nd and 3rd maxillary palpal segments of males of different species of Culisetina reveals that in *Allotheobaldia longiareolata* the palp of males could be regarded more as 5- than 4-segmented. Even in the other species studied, the first category is hardly found and the boundary between the 2nd and 3rd segments of the palps is distinct in an overwhelming majority of cases, that is, categories 2, 3 and 4.

Additionally, Table 1 presents the coefficient of correlation between the type of palps (structure of 2nd+3rd segments) and the maxillary indices of males. A study of the numerical data presented

in the table shows distinct and direct correlation between these structures in all cases, with the exception of *Culiseta setivalva* (and in one case *C. silvestris amurensis* Masl.): the comparatively higher percentage of fusion of the 2nd and 3rd palpal segments corresponds to the low numerical values of the maxillary indices. This pattern reflects the evolution of morphological characters in males of the group Culisetina and is particularly distinctly manifested when correlating all three characteristics in *C. bergrothi* by the normal method: $r_{0.12} = +0.955 \pm 0.008$, as well as by the partial correlation method: (2) $r_{01} = +0.862$.

In all species of *Culiseta* s. str., the length of the palp in males in most cases clearly exceeds the length of the proboscis; the ratio averages from 1.07 in *C. alaskaensis indica* to 1.26 in *C. annulata annulata*. The palp was relatively short only in *C. niveitaeniata*: the ratio of its length to that of the proboscis was 0.98, with a range of 0.94–1.03. The males of subgenus *Culicella* have even longer palps with the ratio of their length to that of the proboscis averaging from 1.17 in *C. setivalva* to 1.55 in *C. silvestris amurensis* (range 1.1–1.8). The palps in *C. melanura* are also long, 1.5 times (1.48) longer than the proboscis. Special investigations conducted by Maslov (1963) showed the exceptional variability of different ratios of male palps; for example, the palpal index which is the ratio of the total length of the first four palpal segments, excluding the last segment, to the length of the proboscis, and the terminal index which is the ratio of 15 the length of the last palpal segment to the total length of the preceding segments. Hence, these indices should never be regarded as conclusive systematic characteristics of a given species or subspecies as some investigators have done (Barraud, 1924; Dyar, 1922, and others; Edwards, 1921a, 1926a; and others; Howard, Dyar and Knab, 1913, 1915; Marshall, 1938; Martini, 1929–31; Peus, 1930a, 1935; Ripstein, 1934, 1935; Theobald, 1901–10; and many others). They are important only as supplementary characteristics for a precise description of a given species.

The measurements of the width of the maxillary palpal segments of Culisetina males are such that the 1st and 2nd are roughly equal in width to that of the proboscis (labium); the 3rd one gradually enlarges apically. The apical segments of the palps may be of the same thickness as the proximal segments (Fig. 9A) or fairly wide (Fig. 9B, C and D). The males of *Allotheobaldia longiareolata* are an exception with short palps and highly spatulate and enlarged 5th and, to a slightly less extent, 4th segments (Fig. 9D). Remote basiconic olfactory sensillae are present on the 2nd + 3rd and 4th pal

pal segments as in other Culicidae (Ivanova, 1960) but only tactile sensillae (trichogen cells) are present on the terminal segment.

Maxillary palps of females are also 5-segmented, but the first two are fairly completely fused, the 3rd and 4th segments normal (4th is the longest), while the 5th is underdeveloped and is found as a small knob or button, often hidden in the pit of the 4th segment. In some species, the 5th segment may even be double in length, as pointed out by Natvig (1948) for *Culiseta annulata* and as mentioned in our data for *C. annulata annulata* and sometimes for *C. bergrothi* and *C. alaskaensis*. The length of the palp averages 16–29% of that of the proboscis, with a range from 10 (in *C. alaskaensis*, *C. glaphyoptera* and *C. morsitans*) to 40% (in *Allotheobaldia longiareolata*). Researchers have not been able to establish any major difference which could be used as a systematic characteristic (Barraud, 1924; Martini, 1929–31; Natvig, 1942, 1948; and others) since the absolute and relative values of the palp in general and of its individual constituents and the nature of the terminal segment are subject to significant variations.

- 16 The pigmentation of the proboscis (labium) and the palp is different and varies from light yellowish-brown to intense black. The color of the scales also varies; a regular alternation of scales (dark and light) often forms a specific design characteristic of given species of Culisetina. In *C. bergrothi*, *C. glaphyoptera*, *C. impatiens*, *C. incidens* and some other species, the proboscis and maxil-

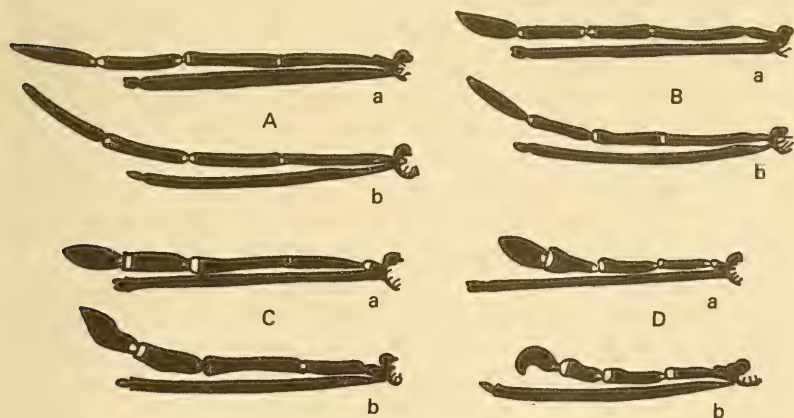


Fig. 9. A few types of male maxillary palps.

A—long, thin; B—relatively long, slightly thickened; C—short, thickened; D—short with broadened (spatulate) apex: a—Lateral view and b—As seen from above (only one palp shown).

lary palps of females are uniformly dark, often with entirely black scales, sometimes with only a slight admixture of light scales, not forming a distinct pattern*. In other cases, (*C. inornata*, *C. annulata*, *C. alaskaensis* and others) the proboscis is distinctly speckled. In *C. fumipennis*, unlike *C. morsitans*, distinct white scales are seen on the female proboscis especially in the middle (Marshall, 1938; Natvig, 1948; and several others).

The maxillary palps in males of some species (*C. bergrothi*, *C. impatiens* and others) are clothed with uniformly brown, dark brown or black scales, sometimes with a rare admixture of golden or even paler scales. In others, the light scales, apart from being fairly intensely gathered all along the length of the palp, form distinct spots and ringlets mostly at the bases of segments. As pointed out earlier, if the 2nd and 3rd segments are fused and the boundary between them is indistinct on the integument, then this boundary often indicates the presence of a light ringlet of scales.

Thorax and its appendages. The segments and the sclerotization of the thorax of insects have been studied in detail by several researchers (Comstock, 1918; Crampton, 1925, 1942; Rioux, 1958; Rubtsov, 1948, 1951, 1953; Shvanvich, 1949; Snodgrass, 1935, 1959; and others).

The structure of the thorax in Culisetina mosquitoes suggests that they hardly require the development of a powerful leg musculature since they have legs of a thin, scaly subtype (Rodendorf, 1951) which provide them a limited capacity to run (see p. 18). On the other hand, the presence of a single pair of wings, as in all dipterans, results in the reduction of the flight musculature of the metathorax. In the course of evolution, the wing-bearing segment, the mesothorax, on the contrary, acquired exceptionally powerful musculature. However, mosquitoes with inadequate mechanical specialization of wing venation (see p. 25) still have a high level of flight perfection. The maximum velocity of their wing movements, from 165 to 311 vibrations/second in females of different species and up to 587 in males (Rodendorf, 1949), lends them strength while rising and provides perfect flight control (Beklemishev, 1944, 1949; Rodendorf, 1949, 1951). Both these features are vitally important to the mosquitoes. The wing velocity of mosquitoes studied for some species of

*The presence of scattered light scales on the female palps of *Culiseta bergrothi* as described by Natvig (1948, p. 168) is considered a characteristic distinguishing it from *C. glaphyroptera* which has uniformly dark palps; this could not be confirmed in the author's material.

Aedes was 75–110 cm/sec and could go as high as 250 cm/sec in short flights (Hocking, 1953). The high maneuverability is essential in their search for food and the high rising capacity with abundant energy enables the female, which has fully sucked blood, to find and reach a safe refuge.

Due to the growth and differentiation of the muscles of the single wing-bearing segment, the mesothorax, the morphological structure of this segment is far more complex than that of the other two. The tergite of the prothorax takes the form of paired pronotal lobes located on the lateral margins of the thorax (Fig. 10, n_1). Both pleural sections of the prothorax, proepisternum and proepimeron (Eps_1 and Epm_1), are well developed. The anterior thoracic spiracle is located in the posterior region of the proepimeron set on a weakly sclerotized membrane. Dorsal to it is the mesothoracic tergum; the basal sclerite lies posteriorly and is bounded ventrally by the mesothoracic proepisternite. The mesonotum ($prsc$, sct , scl and pn) is represented by all four sclerites of the notum proper and the postnotum. Distinctly visible on the dorsal surface are well developed rows of numerous, but not long, acrostichal and dorsocentral setae. The mesonotum of Culisetina, as in most other Culicini, has three sclerites with three groups of strong setae scattered on these sclerites and with rare narrow crescent-shaped scales scattered all over the surface. The postnotum is bare or has a few narrow, crescent-shaped, minute scales, without setae.

The episternum proper is well developed as pleural sclerites of the mesothorax (Fig. 10, Eps_2). It lies under the wing base as a heavily sclerotized pleural region and extends, noticeably broadening downward, to the ventral surface of the thorax. British investigators have named its upper part prealare (Barraud, 1924; Edwards, 1932a; and others); the lower broadened portion is usually called the postalare. From the mesoepisternum proper, the proepisternum is fairly distinctly demarcated in the front and the mesothoracic epimeron in the posterior region (Fig. 10, eps_2 and Epm_2). The mesoepimeron here does not contribute to the formation of the pleural column, while the articulation of the anterior wing margin with the thorax is accomplished by the upper portion of the mesepimeron. Careful examination reveals the boundaries of the basalares (paraepisternite), subalare (paraepimerite) and four wing sclerites, especially the intraalar sclerites which are responsible for the rotatory movement of the wing around the pleural column. The trochanter (tn) adjoins the lower posterior half of the sternopleura. The coxae of the midlegs are joined to the trochanter. Between the coxae of the

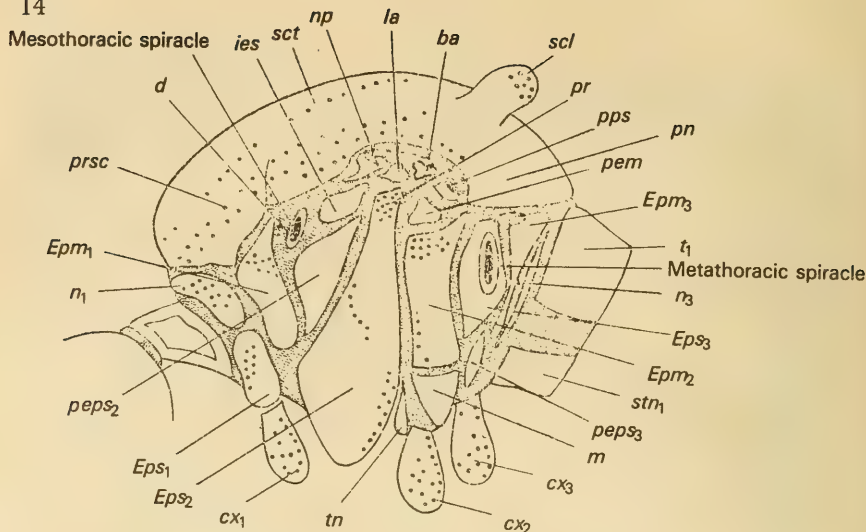


Fig. 10. Thoracic sclerites of mosquito (lateral view).

ba—basianal sclerite; *d*—spiracular setae; *pn*—postnotum; *la*—interalar sclerite; *m*—(epi)meron; *np*—netopteral sclerite; *n1*—pronotum, *n3*—metanotum; *pps*—paraenterite sclerite; *pr*—pleural column; *prsc*—prescutum (acrotergite), *pem*—proepimeron; *peps2*—supraepisternite of mesothorax; *peps3*—supraepisternite of metathorax; *ies*—infraepisternite; *stn1*—first abdominal sternite; *t1*—first abdominal tergite; *cx1*, *2*, *3*—coxae of legs; *tn*—trochanter; *sct*—scutum; *scl*—scutellum; *Epm1*, *2*, *3*—epimerons; *Eps1*, *2*, *3*—episternite.

mid- and hind pairs of legs is the triangular meron (*m*) which is distinct due to its darker pigmentation.

The metathoracic tergite is represented by only a very narrow strip (Fig. 10, *n3*) on each side of the thorax and to these strips is articulated the first abdominal tergite. The narrow supraepimeron (*Epm3*) and supraepisternum lie anteriorly, the latter being subdivided into a small basal sclerite called the proepisternum (*epm2*) of the metathorax (it should be called the infraepisternum) (*eps3*) and a prominent episternum proper (*Eps3*) carrying the metathoracic spiracle posteriorly.

These two pairs of thoracic spiracles control gas exchange with the external environment. As the work of O.N. Vinogradskaya (1953, 1954, 1960)* reveals, the relative dimensions of the spiracles are

*For the structure of thoracic and abdominal spiracles, including *Culiseta annulata* mosquitoes, see also Hassan, 1950; for the neuromuscular mechanism of spiracular operation, see Hoyle, 1959.

directly correlated with atmospheric relative humidity. While studying this phenomenon, Vinogradskaya suggested the spiracular index or the ratio of the percentage of the length of the anterior spiracle (its ventral outer lip when the spiracle is open) to the length of the mesothorax up to the caudal portion of the shield measured in a straight line from the anterior portion of the mesonotum (Vinogradskaya, 1945; Fig. 1).

Study of this characteristic in female *Culisetina* mosquitoes gave similar results for Vinogradskaya's spiracular index, also called the anterior spiracular index (Maslov, 1957a), as well as for the posterior spiracular index and the total spiracular index calculated from the sum of the dimensions of the anterior and posterior spiracles and expressed as a percentage of the length of the mesothorax*. It was necessary to make these supplementary measurements and calculate the three systems of indices because while comparing the measurements of the anterior and posterior spiracles, a compensatory increase in the size of the posterior and reduction in the size of the anterior were observed in mosquitoes with identical mesonotum lengths. The compensatory increase (+) or decrease (-) of the posterior spiracular index in *Culiseta bergrothi* females with corresponding changes of the anterior spiracular index (as a percentage of the total spiracular index, $n=40$) is expressed by the following numerical data:

Deviation	+7	+5	+3	+1	0	-1	-3	-5	-7	-9
No. of specimens	2	3	5	5	12	—	5	5	2	1

The color of the thoracic integument has been described earlier, indicating its different shades of brown, from light yellowish-brown to intense black, depending on the extent of sclerotization. The tergum is invariably more deeply pigmented as the dorsal surface and the sternal pleurae (mesothoracic episternum) are darker than the remaining lateral thoracic regions. The epimeron is particularly so and its dark triangular spot stands out prominently. When the tergum is seen from above even more darkly pigmented longitudinal bands and spots can be detected on the general background. These correspond to the cuticular thickenings in the regions of articulation of the dorsoventral flight musculature.

However, the color and design of the thorax, like those of the

*Dry preserved specimens were investigated.

head, depend not so much on integumentary pigmentation as on the nature and arrangement of scales. The dorsal surface is usually covered by dark golden, narrow, crescent-shaped scales. In some cases these are homogeneous in shade and fairly evenly scattered; in others, more lightly colored and broader scales set among the dark ones sometimes form a very bright and sometimes a less distinct pattern, most often with longitudinal, bent bands extended along the middle and calli of scutum from the anterior margin to the scutellum and onto it. The pattern of light lanceolate scales is particularly distinct dorsally in *Allotheobaldia longiareolata* (Fig. 11, 21 to 24). The postnotum is bare or has scattered, thin, narrow, crescent-shaped golden scales. The lateral thoracic portions are covered with broad lanceolate and leaf-shaped light, often white, scales gathered in the form of spots of variable size, form and disposition, but rare on the lower portion of the sternopleural region and on the epimeron. Spots consisting of white scales are more distinctly visible on the mesoepimerons and in the upper portions of the sternopleural region, especially in *A. longiareolata*.

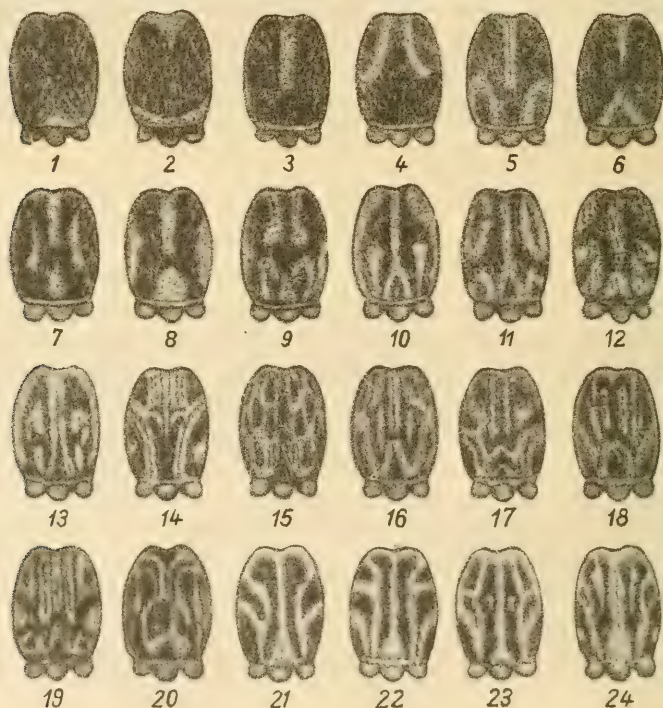


Fig. 11. Types (1-24) of patterns on dorsal surface of the body.

In mosquitoes of the genus *Aedes* from the central European part of the USSR, O.N. Sazonova (1960) noticed a similarity in the pattern formed by the scales on the thoracic calli; she then used this pattern as a significant systematic character. She studied Culisetina mosquitoes (*C. bergrothi*, *C. annulata subochrea*, *C. alaskaensis indica*, *A. longiareolata*, and some others) for this character and found variability in distribution of light scales on the thoracic calli. On this basis she concluded that it is impossible to use this feature as an important systematic character (Fig. 12).

20 The pattern of scales on the dorsal surface is also variable (Fig. 11). It is of particular significance only in *A. longiareolata*, in which this pattern is invariably more distinct due to the presence of very large prominent white scales (Fig. 11, 21 to 24).

The chaetotaxy of the thorax was long used as a systematic character for mosquitoes of the family Culicidae (Fig. 13). One of the most important systematic features distinguishing the genus *Culiseta* from other Culicini genera is the presence of spiracular setae located anteriorly and above the anterior spiracle and turned along the side of the latter (Fig. 13). However, the spiracular setae are present in varying numbers not only in *Culiseta*, but in other genera including *Goeldia* [= *Trichoprosopon*, *Johnbelkinia* and *Shannoniana*, in part], *Tripteroides*, *Sabethes*, *Wyeomyia*, *Topomyia* and *Harpagomyia* [= *Malaya*]. Martini (1931) associated their presence with the body dimensions of mosquitoes. He suggested that in the smaller species the preepimeral setae serve the function of

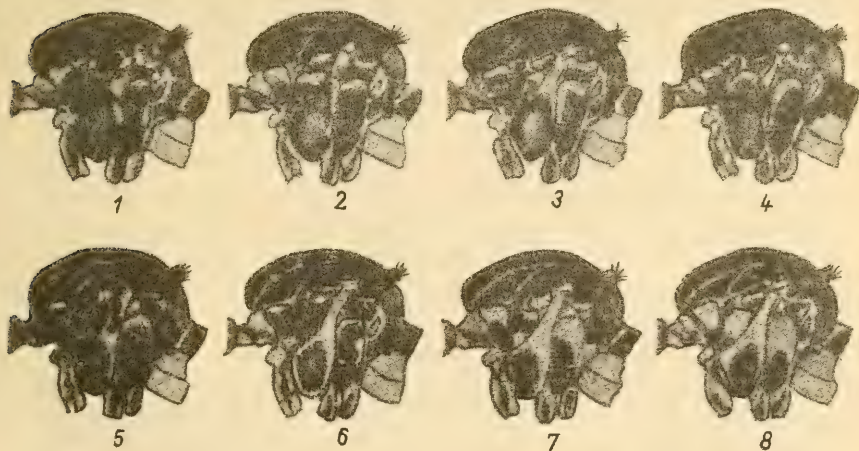
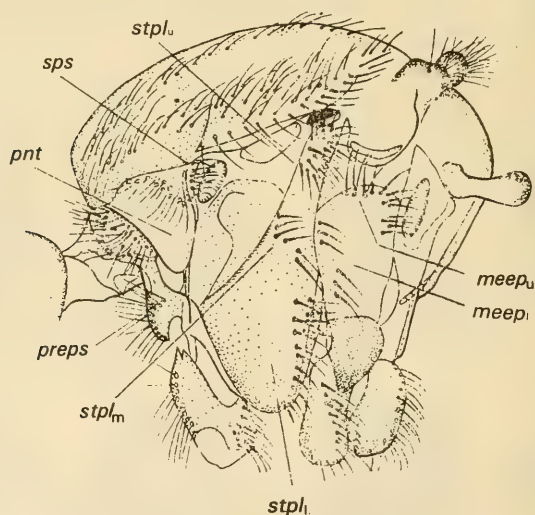


Fig. 12. Types (1 to 8) of thoracic pattern on the calli.

protecting the spiracle from becoming obstructed, while in larger mosquitoes like *Culiseta* and some others, the preepimeral setae do not reach the spiracle and the protective function is assumed by the spiracular setae in these cases. This may be so in some groups of large mosquitoes, but the spiracular setae are found in the smaller forms also (*Uranotaenia*) while, on the other hand, 1–3 spiracular setae, which are hardly adequate to afford any genuine protection, are found in such gigantic mosquitoes as *Psorophora*.

The number of spiracular setae in *Culisetina* is extremely variable: they are few in *Theomyia* (Edwards, 1932a) while there are two in the subgenus *Neotheobaldia* and two or three setae in *Austrotheobaldia littleri* (Dobrotworsky, 1954); a few are also seen in the subgenus *Climacura*. They are fairly numerous only in *Culicella* and *Allotheobaldia longiareolata*, but their numbers vary widely in each species in which they are well developed (Maslov, 1963).

Legs. The long thin legs of mosquitoes are the thin-scaly type, according to B.B. Rodendorf (1951), that is, they are characterized by firmness and skeletal development but have less muscular strength and exhibit slow motion.



21 Fig. 13. Thoracic chaetotaxy of *Culisetina* (after Martini, 1929–31).

Setae: *hm*—humeral [not shown]; *pnt*—pronotal; *preps*—propleural (pre-episternal); *sps*—spiracular; *stpl*—sternopleural (upper, middle and lower); *meep_u*—upper mesoepimeral; *meep_l*—lower mesoepimeral.

21 The uniaxial articulation of the femur and tibia is considered the rough topographic center. In legs bent at this joint, the femur and tibia are turned to each other invariably on the lower side. The opposite and parallel side then becomes the upper side and the two perpendicular surfaces form the anterior and posterior portions. In an analogy of these surfaces, the legs and tarsal claws are designated anterior and posterior. The length of the leg segments is measured from their base (articulation with the preceding segment) to the apex along the upper side: the length of the last, fifth, segment is measured from its base to the base of the claws. The width of the rings in mosquitoes, when present, is established by the relative thickness (diameter) of the segment in the region of its disposition.

The legs as a whole and their individual segments are very long. They are 1.5 times or more the length of the proboscis and body length of the mosquito. Like other morphological characters, the length of the legs varies in a wide range, not only in different subspecies or related species, but even in the same species.

The dimensions of individual segments are also variable. In males and females, the length of the tibia as a rule exceeds that of the femur in all three pairs of legs. The proximal tarsal segments on fore- and midlegs of females and males are shorter than the length of the femur, 65–70% of its length (varying from 50 to 85% in the different species). The proximal segments of the hindlegs are distinctly longer. In females, in most cases, they are almost equal to the length of the femur, while they are even longer in males. The ratio of the fourth and fifth segments varies greatly in males and females; the segments are the same length or the last one is slightly smaller than the penultimate segment on the fore- and midlegs of females. In the hindlegs of females, the terminal segment is noticeably shorter than the fourth; this is even more distinct in males, while the fourth segment of the fore- and midleg tarsus is almost half compared to the fifth. This is due to the special structures and functions of the terminal segments of the fore- and midlegs with which the male holds the female during copulation.

Specieswise differences in proportions of leg segments and their total length are not so significant as to serve as factors of primary systematic importance; and, within a given species or subspecies, these factors vary further. Among *Culiseta alaskaensis alaskaensis*, the forelegs of females show the following dimensions of leg segments: 100:112:79:29:18:10:12 (western Europe) and 100:102:62:25:17:10:10 (Canada). Among the females of *Allotheobaldia longiareolata* of India, the ratio of different segments in the forelegs

is 100:126:66:26:15:9:11 and among Palestinian species it is 100:116:60:26:14:9:9. The segments of hindlegs among the females of
 22 Indian mosquitoes of this species are in the proportion 100:107:72:38:18:12:9 and among the Palestinian 100:105:79:46:29:14:11.

Indices like the tarsal or tibiotarsal index are also variable. The value of the tarsal index (ratio of the length of the first segment to the length of the remaining four) used by Martini (1929-31), Dyar (1922), Marshall (1938), A.A. Shtakel'berg (1937); and others to differentiate the species of subgenus *Culicella* and the value of the tibiotarsal index (ratio of the length of the first tarsal segment to that of tibia), cannot be regarded as reliable systematic features (Maslov, 1963).

It does not, however, follow from the above that none of the indices and segment ratios of legs examined so far can be used as suitable systematic characters. They could be used as supplementary and sometimes as extremely valuable characteristic features while describing a given species, subspecies and so on, especially while studying the morphological variations of mosquitoes in diverse environmental conditions.

Different types of setae, spines, spinules, scales and other structures of cuticular origin grow to various extents on all leg segments. Small ellipsoidal coxae are densely covered by minute setae and scales varying in form from narrow and lanceolate to broad and leaf-like. Among them are several long setae. Similar to this is the basic pattern on the small cone-shaped trochanter.

The femora are similarly covered by numerous setae, small spines and scales all along their length. The setae concentrated at the apices form a hairy pubescent femur around the articulation with the tibia. While essentially similar, the tibiae differ in having much larger and sharper spines as well as setae and minute spinules all along their length. In some species of *Culisetina*, the short, sharp spinules form 2 distinct longitudinal rows, each consisting of 30-50 spinules on the lower surface of the foretibia. Such rows of spinules (more characteristic of the first and fourth segments of the foretarsi, see below) are seen in *Culiseta alaskaensis*, *C. annulata* and *C. bergrothi*, but not detected in *C. glaphyoptera*, *C. inornata*, in members of the subgenus *Culicella* and in *C. melanura* and *Allotheobaldia longiareolata*. In all *Culiseta*, at the apex of the lower surface of the hindtibia, there is a prominent transverse row of 8-15 strong setae set as though in a "palisade" of thin, very short setae, as a tibial spur (tibial scraper or "putzapparat" of Martini and Natvig, Fig. 14). Although this tibial spur is more distinctly formed on the hindlegs,

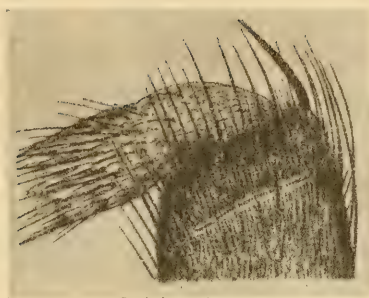


Fig. 14. Tibial spur.

it is found quite often, although less distinctly, in the other two tibiae. On the anterior ventral surface of the tibia, a concentration of minute setae is found at the apex apart from the spur, and some prominent spines are found on the ventral surface at the apex itself in the region of articulation with the first tarsal segment.

Apart from scales, minute spinules and setae are dense and obscure the tarsal segments. Two rows of short, sharp spinules stand out distinctly below the first and second segments of the foretarsi. These rows are apparent even on the foretibiae, but are more characteristic at the above location on the foretarsi. Although varying in number (40–70 in each row on the first segment and 15–35 in the second), their sharpness and regularity have been detected in all *Culisetina* studied. They are weakly developed in *Allotheobaldia longiareolata*, but totally absent in *Culiseta melanura*. Interestingly, they are most clearly seen in mosquitoes of the subgenus *Culicella* which do not have rows of spinules on the foretibiae. In some species (*Culiseta annulata* and *C. bergrothi*) similar and no less distinct rows of spinules are visible even on the proximal segments of the midlegs, but these have never been seen on the other segments or on the hindlegs. The abundance of setae and some strong spines are apparent on the dorsal and ventral surfaces at the apex of each segment of all tarsi, especially at the junction between the segments.

The terminal five segments of the tarsi, as pointed out, differ greatly in structures on the fore- and midlegs of males. For copulation, they are significantly larger and have a group of 6 to 10 firm, flexed spines on the ventral surface of the enlarged base (Fig. 16). These segments have powerful crenated claws. The terminal segments of the tarsi of the hindlegs in males, like the female tarsi, are usually cylindrical in structure with simple claws. These differences

in claw structure have long been used as a systematic character in the claw formula (Howard, Dyar and Knab, 1913, 1915; Martini, 1929-31). In the males of all Culisetina mosquitoes (Fig. 16), this formula is numerically expressed as 2:1, 2:1, 0:0 and in females (Fig. 15) as 0:0, 0:0, 0:0, that is, the foreclaws in the fore- and midtarsi of males have two teeth and in the hindtarsi one tooth; the claws are simple, without teeth, on the hindtarsi of males and in all legs of the females. Thus, the work of Martini (1929-31) (pp. 204 and 218) showing that the males of *Culiseta alaskaensis* and *C. morsitans* have claws conforming to the formula 2:1, 1:2, 0:0 appears to be erroneous.

A long hairy empodium is present at the distal end of the fifth segment between the bases of the claws (Figs. 15 and 16).

Depending on the general body color of the mosquito, the color of the legs varies with the type of scales covering the integument. The color varies from dense black (*C. bergrothi* and *C. melanura*) to light yellowish-brown (*C. annulata subochrea*, *C. alaskaensis indica*, *Allotheobaldia longiareolata*, and others) with intermediate brown shades of different intensities. In some cases, the scales are uniformly dark and then no pattern appears on the legs (*C. bergrothi*, *C. glaphyoptera*, *C. impatiens*, *C. inornata* and *C. melanura*, Fig. 17). A very light, often pale, distal surface of the femora is observed in these species.

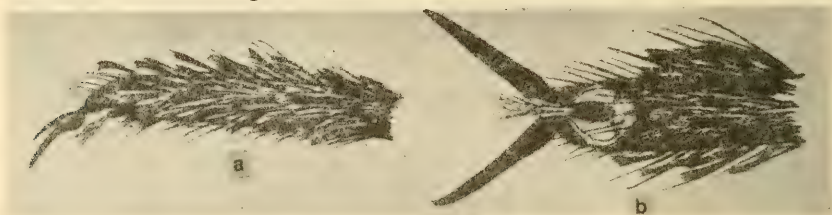


Fig. 15. Tip of female tarsus.
a—lateral view; b—ventral view.

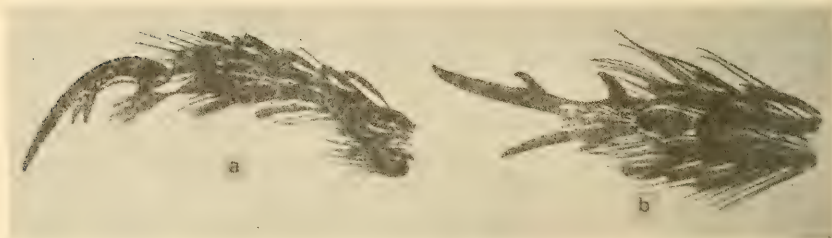


Fig. 16. Tip of male tarsus.
a—lateral view; b—ventral view.

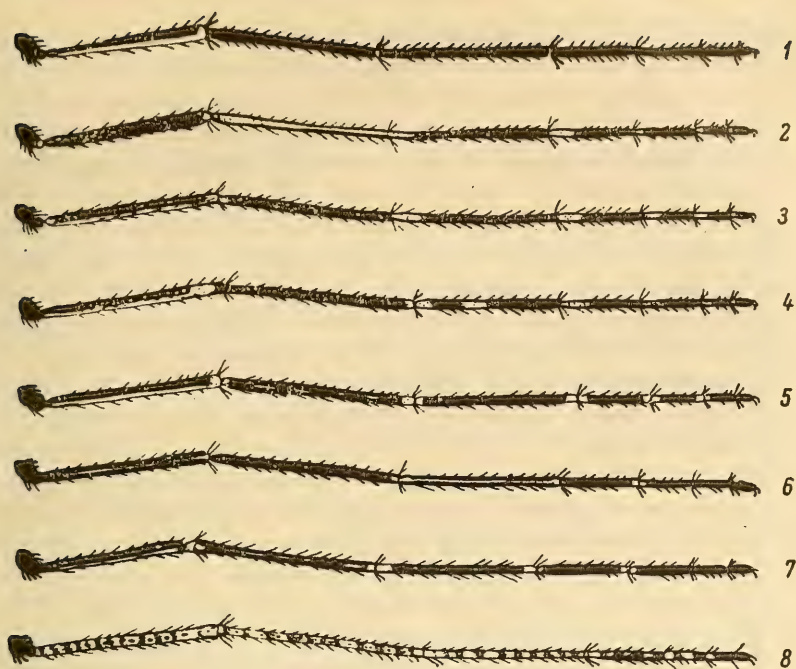


Fig. 17. Types of leg patterns.

1—*Culiseta bergrothi*; 2—*C. particeps*; 3—*C. alaskaensis*; 4—*C. annulata*;
5—*C. fumipennis*; 6—*C. silvestris amurensis*; 7—*C. morsitans* and 8—
Allothobaldia longiareolata.

In other mosquitoes, the femora are distinctly spotted anteriorly due to the presence of numerous white scales interspersed among a mass of dark ones (*C. alaskaensis*, Fig. 17, 3). In some species, the femora anteriorly have fused spots consisting of light scales forming a subapical, small, light ring in *C. annulata* (Fig. 17, 4). In some species, light scales are seen on the femora anteriorly; they may be barely noticeable or form a distinct longitudinal light band (*C. silvestris amurensis*, Fig. 17, 6). In *Allothobaldia longiareolata*, the femora anteriorly (and all other leg segments with the exception of one or two terminal tarsal segments) have alternate spots of white and dark white scales interspersed among a mass of dark ones (*C. alaskaensis*, Fig. 17, 3). In some species, the femora anteriorly have fused spots consisting of light scales forming a minute, light subapical ring in *C. annulata* (Fig. 17, 4). In some species, light scales are seen anteriorly on the femora; they may be barely noticeable or form a distinct longitudinal light band (*C. silvestris amurensis*, Fig. 17,

6). In *Allotheobaldia longiareolata*, the femora anteriorly (and all other leg segments with the exception of one or two terminal tarsal segments) have alternate spots of white and dark scales creating a typical spotted form (Fig. 17, 8). With a few exceptions, the extreme apex of the femur is covered with light scales forming a typical knee spot.

In some cases the tibiae (as shown in Fig. 17) are uniformly dark (*C. bergrothi*, *C. impatiens*, *C. melanura*, and others); in others, they are spotted as in *C. alaskaensis* or have fused spots of light scales as in *C. annulata* or light longitudinal bands. The longitudinal band on the tibia stands out distinctly in *C. bergrothi*, *C. morsitans* and some other species (*C. setivalva*). Like the femora, the anterior portion of the tibia is usually clothed with white scales in almost all species studied.

The tarsi of Culisetina mosquitoes (excluding *Allotheobaldia longiareolata* mentioned before) can be divided into three main groups on the basis of the type of their color patterns (Fig. 17). Some species (*Culiseta bergrothi*, *C. glaphyoptera*, *C. impatiens*, *C. melanura*, and others) are entirely dark without rings (Fig. 17, 1). Other species (*C. alaskaensis* and *C. annulata*, Fig. 17, 3 and 4) are characterized by fairly broad rings at the base of all of the segments, with the exception of one or two apical ones. The relative width of these rings* varies significantly from an extremely reduced condition (less than one-half of the thickness of the segment) to broad (2-3 times the thickness of the segment). The third basic type of tarsal pattern is found in mosquitoes of the subgenus *Culicella*. This group has narrow rings at the joints, that is, the apex of the preceding and the base of the succeeding segments (Fig. 17, 5 to 7). A wide range of variation is found here too: in *Culiseta morsitans*, the ring in some tarsal segments may be absent or may be only apical (in the foretarsi) or only proximal but more often, the first and the second are found together, at least on the long proximal segments of the tarsi.

In some species, longitudinal light bands are seen on the proximal tarsal segments and on the tibia, in *C. silvestris amurensis* and, especially distinctly, in *C. setivalva*.

Wing. The study of wings and flight of insects began over a century ago and by now the data are very advanced. We will not discuss the history of this subject, which has been adequately detailed

*The ratio of ring width to the thickness of the segment in the region of its location.

in the literature (Martynov, 1924; Prochnow, 1928; Rodendorf, 1949, and others). However, we do mention some studies pertaining particularly to mosquitoes of the family Culicidae. The relative wing dimensions, the nature of venation and so on have been studied by several investigators (Blanchard, 1905; Christophers, 1933; Christophers and Barraud, 1924; Dyar and Knab, 1909; Edwards, 1921a, 1926a and 1932a; Martini, 1929-31; Matheson, 1944; Snodgrass, 1959). Particularly interesting are the works of Beklemishev (1944) and others on wing structure in relation to flight and several investigations on wing variations: the works of Dyar (1916, 1924[b]), Kazantsev (1930, 1931), Marshall (1926) and Maslov (1957b; and others).

The evolution of the wing in dipterous insects proceeded toward an increase in relative dimensions, that is, elongation of the wing and an increase in its strength achieved by the reinforcement of the anterior margin and at the same time a rearrangement of the plane of the wing sclerites with progressively increasing aerodynamic properties (Rodendorf, 1949, 1951). The strengthening of the anterior margin, or the costal area, is ensured by a greater development of the veins of the anterior wing with a simultaneous reduction of median and posterior veins. The members of families Agromyzidae, Chloropidae, Tabanidae and others, and, among longicorn [nematoceran] dipterans, the biting midges of the family Ceratopogonidae and the midges of the family Simuliidae have such wings with sclerotization in the costal area. The wings of Culicidae [mosquitoes], including Culisetina, are in the special scaly class (culicoidal) (Rodendorf, 1951) in which there is an absence of perceptible specialization of the wing surface but a nearly typical primitive type of venation is preserved (Fig. 18).

The costal vein (costa —C)* is well developed all along the anterior margin of wings in mosquitoes and is significantly thickened along the anterior margin. The subcostal vein (subcosta—Sc) extends from the wing base far beyond its middle region parallel to the costa and merges with it. The subcosta measures about 60-70% of the wing length. The base of the subcostal vein itself is hidden in the basal region under a broadened manubrium of the radial vein. The latter vein (radius—R) consists of four branches: the first unbranched one is the radial vein proper (R₁). It extends from the base to the apex of the wing parallel to the anterior margin. From this vein branches the common branch for all other radial veins, that is, the

*Here and subsequently the letter symbols universally used to designate wing veins and their Russian nomenclature are given simultaneously.

radial sector (sector radii—Rs). From it, in turn, branches, initially, the posterior radial vein formed by two fused veins (R_{4+5}). Later the common branch of the radial sector forms a fork (R_2 and R_3). Relative length (R_{2+3} , R_2 and R_3) has often been used as the systematic character in the classification of Culisetina and other mosquitoes (Edwards, 1932[a]; Martini, 1929–31; Matheson, 1944; Natvig, 1948 and many others).

The median vein (media—M) runs without branching almost all along the wing length and only close to its outer margin forms the fork M_1 – M_2 analogous to the fork R_2 – R_3 used extensively in systematics. Furthermore, the distance from the radio-medial (R-M) cross-vein to the fork proper is regarded as the length of the trunk of this fork (M_{1+2}). The third medial vein (M_3) is set off from the common trunk and joins the next, that is, the cubital vein (Cu). This has thus been regarded as a branch of the cubital vein, now commonly accepted by most researchers. However, the investigations of B.B. Rodendorf (1946) showed that the first cubital vein is actually the third medial and hence the medio-cubital vein is not actually that, but serves as a base for the third medial (central) vein. However, to

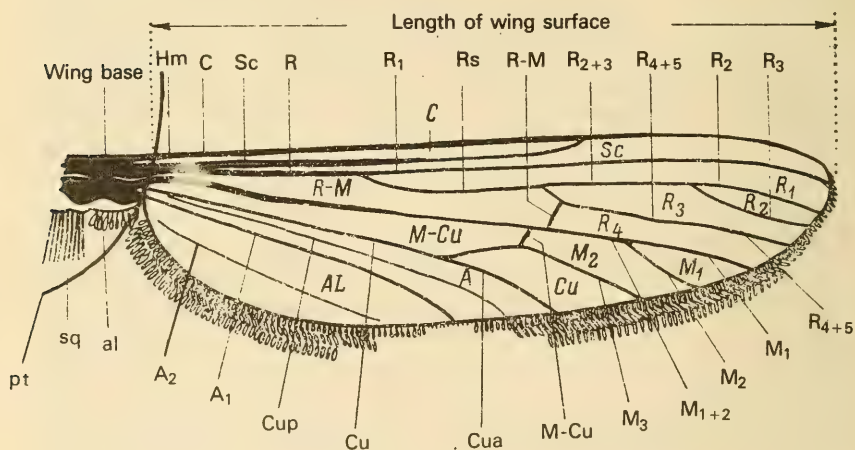


Fig. 18. Structure of wing.

Wing veins designated by upper case outside the wing surface; wing cells designated in italics within the cells. al—alual; AL—anal lobe; A_1 and A_2 —anal; C—costa; Cu—cubitus; Cua and Cup—cubitus anterior, cubitus posterior; Hm—humeral; Sc—subcosta; R_1 , R_2 , R_3 —radius and its branches; Rs—sector radii; R-M—radio-medial; M_1 , M_2 and M_3 —media and its branches; M-Cu—medio-cubital; pt—pterygium; sq—squama.

avoid any possible misunderstanding, the author regards it as expedient to call the third medial vein by its name (M_3) while retaining the old name, medio-cubital vein (M-Cu), for the cross-vein.

In this case, the cubital (cubitus—Cu) becomes a single vein without any branch. This cubital vein represents the anterior one (cubitus anterior) since the posterior one (cubitus posterior) in *Culisetina* mosquitoes and in many other dipterans is not developed and is preserved only in the form of a fold between the lone cubital and anal veins. From among the anal veins (analis—A) only one, the first (A_1), is retained while only a distinctly visible tiny fold is seen of the second.

In addition to the above veins (R-M and M-Cu), we mention the humeral crossvein (H) joining, at the base of the wing surface, the costal vein with the subcostal. This, with other structures, represents the boundary between the basal and wing surfaces. The membranous sections separated by the veins—wing cells—as shown in Fig. 18 are named in accordance with the names of the corresponding veins forming the cells. The posterior, lowermost portion of the wing is called the anal lobe.

The wing base providing excellent flying properties to mosquitoes and many other insects capable of active flight with high velocity and directional control, represents a system of thickened and proximated vein bases—their manubria—with membranes between them and the development of the postanal portion of the wing membrane in the form of a pterygium, wing scales and often thoracic scales. The humeral vein joining the costal with the subcostal vein, forms the boundary of the base; the next boundary is the phragma or fold, an outgrowth or crossvein between the bases of the radial and cubital veins; the last boundary is the pit between the inner margin of the wing surface proper, the anal lobe, and the pterygium forming the basal setup. In *Culisetina* mosquitoes, this vital portion of the wing base (Fig. 19) is extremely well developed. It has a significantly thickened base (manubrium) of the radial vein, completely obscuring the base of the subcostal vein. On the basal portion of the radial vein, named by British investigators as the stem vein (Barraud, 1924; Edwards, 1932a) near the large phragma, there is a group of short setae, the radial setae* (Fig. 19, X) (remigium, according to

*These are called the remigial setae by later authors, i.e., Harbach, R.E. and K.L. Knight, 1980. Taxonomists' glossary of mosquito anatomy. Plexus Publ. Co. [Editor].

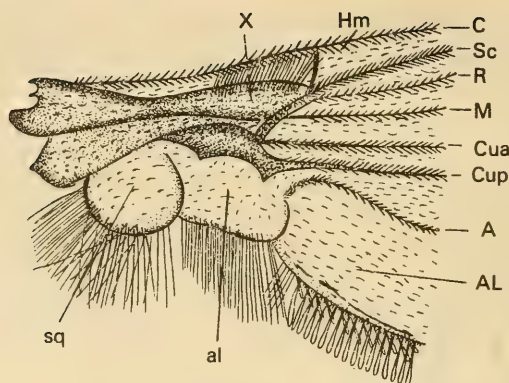


Fig. 19. Wing base of *Culiseta*.

X—Remigium. Remaining labels are the same as in Fig. 18.

British authors) in the form of a pointed process. The radial setae are
 28 absent in the other members of the family Culicidae, except Culiset-
 ina, and thus represents one of the vital systematic features of the
 subtribe Culisetina*. The number of setae on the lower surface of
 the remigium** is often several dozen; their growth on the upper
 surface of the wing is poor.

The thickened base of the anal vein covers the base of the cubitus
 vein and serves as the second large arm of the base. Along its poste-
 rior margin the wide pterygium has a row of narrow, lanceolate
 scales. The wing alulae (squamae) have long setae. The thoracic
 setae are absent in Culisetina as in other mosquitoes of the family
 Culicidae.

Without repeating the overall wing dimensions and forms dis-
 cussed elsewhere, some details of venation and its variability in the
 different species and groups of Culisetina are discussed below.

The subcostal vein extends from the wing base parallel to the
 costal vein and joins it roughly at the boundary of the second vein
 and the last one-third of the wing length. The ratio of the length of
 the subcostal vein, measured from the humeral plate to the junction
 with the costal, to the length of the wing surface expressed as a
 percentage is called the subcostal index or the index of the subcostal
 vein.

*The African *Theomyia fraseri*, in which the remigium is absent, is an exception.

**Considered as the lower surface of the subcostal vein by most later authors
 [Editor].

The radial vein R_2 is well developed. Beginning at the basal portion, it runs through the whole surface of the wing parallel to the costal vein and ends at the wing apex forming the boundary between the anterior and outer margins of the wing (the ptermen). There is significant variability in the sector radii (R_s) and their branches. In most members of Culisetina, the sector radius branches out smoothly from R (Fig. 20a, 1). In other cases, R_s begins independently and is joined to the radial vein with a distinct crossvein which could be called the proximal-radial crossvein, Pr (Fig. 20a, 2, 3). The base of the sector radii is sometimes shifted some distance from this crossvein (Fig. 20a, 2); sometimes the displacement is toward the base (Fig. 20a, 3). An examination of these structures leads one to agree with Yu.M. Zalesskii (1943) that R_s is far from invariably an actual branch of the radial vein, but is an independent structural element of the wing. He named it "antemedian". However, all branches of the sector radii in mosquitoes (R_2 , R_3 , and R_{4+5}) represent veins of the same sign as the radial vein itself, that is, upper veins (Rodendorf, 1946) and this supports the stated view and the corresponding terminology.

The last radial vein R_{4+5} in some cases branches smoothly from the R_s (Fig. 20b, 1) and in others is connected to the R_s with a distinct crossvein called the distal-radial crossvein Dr (Fig. 20b, 2, 3). Sometimes this vein and the radio-medial vein serve as a continuation of each other (Fig. 20b, 2); however, sometimes it is shifted distally (Fig. 20b, 3) or proximally from $R-M$.

These variations of the proximal and distal-radial crossveins are not detected to the same extent in various species and groups of

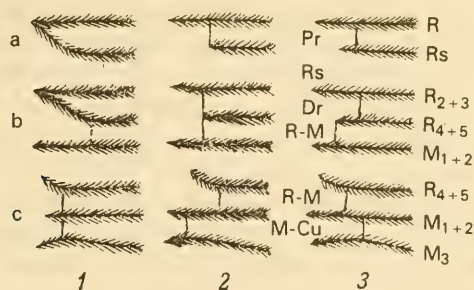


Fig. 20. Variation of some wing veins.

a, b and c—wing sections (in the horizontal plane); 1, 2 and 3—types of venation (along the vertical plane), Pr —proximal-radial and Dr —distal-radial crossveins. Remaining symbols as in Fig. 18.

Culiseta. Therefore, this feature can be used in intraspecific systematics. However, it should not be assigned undue importance since, within a given species (for example, among *Culiseta bergrothi*, *Allothoebaldia longiareolata* and others), almost all the above variations of the disposition of these veins are found.

In the systematics of *Culiseta*, the relative dimensions of radial and medial forks are often used (Dyar, 1924; Howard, Dyar and Knab, 1913, 1915; Martini, 1929-31; Theobald, 1901-10, 1905). Further, many divergent aspects of these values have been found in the reports of different investigators for the same species of mosquito. This is due not only to actual variations, but to differences in the methods of study. Some special indices should be established for purposes of accuracy and comparability of data. The ratio of the stem R_{2+3} to the length of the second radial cell bounded by the veins R_2 and R_3 , expressed as a percentage, is called the radial fork index. The length of the stem R_{2+3} is measured from the point of branching of R_{4+5} (or from the distal-radial crossvein) to the branching of R_2 - R_3 ; the length of R_3 is considered the length of the second radial cell. The medial fork index is the ratio (also as a percentage) of the stem length M_{1+2} to the length of the first medial cell bounded by the veins M_1 and M_2 . The length of the stem M_{1+2} is measured from the level of the medio-cubital crossvein M-Cu to the fork M_{1+2} ; the length of M_2 is taken as the length of the cell.

The studies of these indices in males and females of different species of Culisetina (Maslov, 1963) have revealed their exceptional variability. Nevertheless, in some cases, significant differences are found in their values for related species and subspecies. Hence, these values can be used in systematics, for example, when comparing the males of *Culiseta alaskaensis alaskaensis* and *C. alaskaensis indica*, and so on. However, even here, this character should be used with caution. It is possible that extensive study of such mosquitoes as *C. incidens* and *C. inornata* will reveal a wider range of variability of fork indices, especially if mosquitoes from different regions of the range are studied.

In the systematics of Culisetina, great importance is assigned to the nature of the relative disposition of radio-medial and medio-cubital crossveins (R-M and M-Cu). Many investigators regard this feature as a basis for distinguishing the subgenus *Culiseta* s. str. from *Culicella*. In the former, the crossveins fuse with one another, while in the latter R-M is significantly shifted distally from M-Cu (Barraud, 1924; Dyar, 1924b; Howard, Dyar and Knab, 1913, 1915; Edwards, 1932a; Marshall, 1938; Martini, 1929-31; Natvig, 1948;

Peus, 1930a; Shtakel'berg, 1937; Theobald, 1901-10). The assigning of absolute values for this feature, as in several other systematic characteristics, led to confusion. There are some references in literature on deviations from this rule, that is, differences of opinion on crossveins. Peus (1930a) pointed out that in *Culiseta annulata subochrea*, the R-M could be slightly more proximal and slightly more distal in relation to the M-Cu. This has also been suggested by Dyar (1917)* in *C. inornata* and by Howard, Dyar and Knab (1915) in *C. particeps*.

- 30 A special study of this aspect demonstrated great variation of the index of crossveins. This index characterized the relative disposition of the crossveins and denoted the ratio of the distance between R-M and M-Cu to the length M-Cu. If the veins fuse with each other and the distance between them is zero, the value of the index is taken as zero (Fig. 20c, 1); if the radio-medial vein is shifted distally, as is typical of *Culicella*, then the value of the index is positive (Fig. 20c, 2); if, however, the R-M is proximal to the M-Cu, then the value of the index is negative (Fig. 20c, 3). The results of investigations conducted by Maslov (1963) showed that only in male and female mosquitoes of the subgenus *Culicella* the index of crossveins is invariably positive and much higher than in *Culiseta* s. str. But even in such typical species of the subgenus *Culiseta* as *C. alaskaensis*, *C. glaphyroptera* and others, the value of the index varies from zero or -0.5 to +1.0. In *C. bergrothi* the positive value of the index may be even higher, from -1.4 to +1.5 in females and males. The range of variation is even wider in *Allotheobaldia longiareolata*, from -1.0 to +2.5 in males and from 0 to 2.0 in females. Thus, this character alone, without considering its variability, is hardly useful in the study of the systematics of Culisetina.

Depending on the disposition of the medio-cubital vein relative to the radio-medial, its ratio vis-à-vis to the third medial vein M_3 also changes. In most mosquitoes, M-Cu enters M_3 where it forms a steep bend, but sometimes, especially in *Allotheobaldia longiareolata*, M_3 does not form such a sharp angle, but turns smoothly and then the medio-cubital vein merges with M_3 distinctly distal to this smooth flexure.

The wing surface is covered with different types of scales, setae and microtrichia. The wing surface is covered with extremely tiny

*Not listed in References [Editor].

setae*, microtrichia, which hardly measure $10\ \mu$ long. Scales congregate where dark spots are present (forms R_2 - R_3 , M_1 - M_2 and cross-veins). Microtrichia also concentrate in this region. Here too, the wing itself is somewhat darkly pigmented.

Slightly longer (10 - $12\ \mu$) microtrichia are located along the outer margin and anal lobe of the wing and form a portion of the fringe. On the veins, especially the anterior ones, we find numerous short setae interspersed among dense scales. Similar setae are also found on the basal arm and, as we have noted, there are dense brushes of long setae, the remigium [remigial setae] at the base of the radial [and subcostal] veins.

There are two types of scales covering the wing veins: prominent, long, narrow and lanceolate and very small, slightly leaf-shaped. The latter are grouped mostly on the anterior wing veins, while the lanceolate type are seen on the posterior veins. However, even in this respect, there are many differences. The concentrations of narrow, lanceolate scales in the form of spots and the variability of this character in different Culisetina has been discussed earlier (Fig. 4). The original structure of the wing fringe consists of four different elements (not three as stated by Rodendorf, 1951, p. 56) (Fig. 18). The first of these are the microtrichia densely set along the wing margin. Between them are comparatively short (about $20\ \mu$) and some obliquely set, narrow, lanceolate scales. Further, there are two rows of irregularly alternating, very long (40 - $50\ \mu$), narrow, lanceolate scales, with a long stem and other similar ones with a very short stem and from there, scales of shorter length (30 - $40\ \mu$). There is a row of usually narrow, lanceolate, sometimes almost linear, scales
31 along the posterior margin of the pterygium. There are usually a few hair-like or linear, more rarely very narrow, lanceolate scales on the wing scale [tegula].

We know that the second pair of wings in mosquitoes has been transformed into halteres; this does not differ in Culisetina from other members of Culicidae.

Abdomen and its appendages. The abdomen of mosquitoes is in the form of ten segments of which the first seven are normal and the last three are somewhat altered. Moreover, as in many other dipteran males, in the pupal stage they turn 180° around the longitudinal axis of the body so that the tergite is turned toward the sternite and

*These are actually minute, tapered spicules [Editor].

vice versa. The composition of the male abdomen* is shown as follows:

I	II	III	IV	V	VI	VII	8	9	10
1	2	3	4	5	6	7	VIII	IX	(X)

and of females:

I	II	III	IV	V	VI	VII	VIII	IX	X
1	2	3	4	5	6	7	8	9	10(11)

Each abdominal segment consists of heavily sclerotized tergal and sternal plates joined by membranous pleurae. This enables the abdomen of mosquitoes to greatly expand. This phenomenon is vitally important in the life of the female which, while sucking blood, sucks into the stomach as much blood as its own weight or even more. The abdomen can expand in width as well as in length. As in other insects, the ability of the abdomen to extend longitudinally is facilitated by secondary sclerotization (Shvanvich, 1949; Snodgrass, 1944, 1959; and others) resulting in typical intersegmental articulations.

Heavy sclerotization makes the abdominal tergites darker than the sternites. However, the visible color of the abdomen depends not so much on the pigmentation of the integument as on the nature of the scales; these are invariably darker and brighter and usually form different patterns on the tergites. Only in rare instances are the scales of the tergites uniformly dark, for example, in *Culiseta melanura* (Fig. 21, 1). Often, on a generally dark background, we find scattered light scales and the tergites acquire a speckled appearance (Fig. 21, 2-4). As these illustrations indicate, the number of interspersed light scales varies widely not only in different species but within a given species.

In many Culisetina (*Culiseta annulata*, *C. bergrothi*, and others), the light scales are grouped into somewhat broad, light bands at the base of each tergite (Fig. 21, 5, 6). Often the uniformity of the band is disturbed in such a way that more light scales appear to be on the sides of the tergite and fewer toward the median longitudinal area (Fig. 21, 12). Further such change includes the disappearance of the light scales along the middle of the tergite base, with only dorsolat-

*The true tergites are shown by Roman letters and sternites by Arabic numerals; reduced segments have been shown in parentheses.

eral light triangular spots apparent instead of a band (Fig. 21, 11). In others, on the contrary, the lateral areas of the bands are reduced and the pattern takes the form of a light triangular spot with the apex turned toward the posterior margin of the tergite (Fig. 21, 9, 10).

32 Like the varying nature of spots, the relative width and length of light bands varies not only in the different species of *Culisetina*, but in the same species.

In most *Culisetina* mosquitoes, the monotypical nature of the pattern is essentially preserved on all the abdominal tergites, but is more distinctly manifested on the middle segments, the 3rd to the 6th segments. In some instances, the individual abdominal tergites have a prominent and specific type of pattern (Fig. 21, 7, 10, 15, 16).

The brightness of the tergite patterns is due not only to the quantitative number of dark and light scales, but to the basic nature of the color of the scales themselves. In some instances, the dark

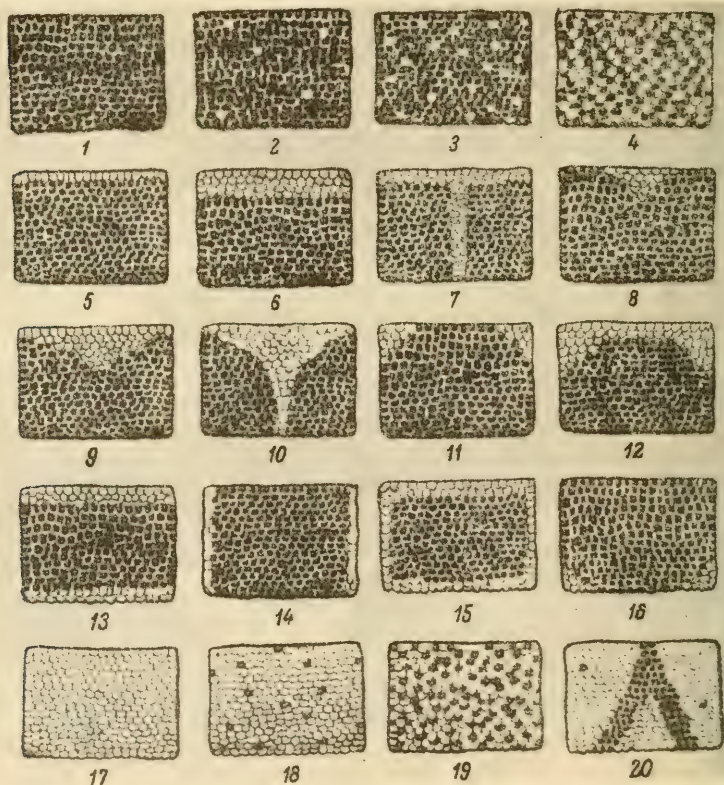


Fig. 21. Types (1-20) of pattern of abdominal tergites (1-16) and sternites (17-20).

scales are black, dirty brown or dark brown (classes 1, 2 and 3 of Fig. 21) while the light ones are pure white; the pattern then is sharply discernible. In others, the dark scales are brown, light brown or even yellowish-brown (classes 4, 5, 6), while the light ones are dirty white or pale ocher; the pattern then appears obliterated or smudgy.

The color and pattern of abdominal sternites are far more monotypic. They are usually covered with uniform, pale, ocher or dirty white scales. The presence of a distinct pattern of dark scales grouped in the form of the English letter V with the pointed end upward (Fig. 21, 20) on the median sternites (3rd to the 5th) of the abdomen has been mentioned in literature as an excellent systematic characteristic distinguishing *Culiseta fumipennis*. An extensive study of *Culiseta* mosquitoes showed that a similar pattern is seen in *C. setivalva*. This was responsible for the erroneous original identification of the latter species from the southern coast of Crimea as *C. fumipennis* (Velichkevich, 1931). A study of the other members of the subgenus *Culicella*, especially of *Culiseta litorea*, showed that the same V-shaped pattern is found in this species too (Rioux, 1958; and others); sometimes it is found among *C. morsitans* also.

The forms of scales covering the abdominal tergites are homogeneous; the scales are fairly large, broadly lanceolate or leaf-shaped with a rounded or more often straight, free margin. Long and short setae are present on tergites and sternites apart from the scales. These setae are denser along the lateral margins of each tergite.

Genital appendages. The eighth or pregenital segment in *Culisetina* males is smaller than the first seven segments, while in females there is no difference. With the last two segments in males, the eighth one turns 180° along the longitudinal axis of the body and the tergite and sternite change places topographically. In other respects, the eighth segment develops in the same way as the preceding ones and is covered with similar scales and setae. Only in some species of *Culiseta* is the median portion of the eighth tergite of males extended distally into a fairly distinct lobe bearing varying numbers of short, strong spines in each species. The presence or absence of a lobe with spines on the eighth tergite and the number and variability of spines could be used as an additional systematic feature for the identification of species of *Culisetina* mosquitoes.

The ninth genital segment in males is complex with numerous and divergent appendages. The hypopygium is the genital structure significant in the systematics of insects. For a long time this structure has attracted the attention of investigators in the field of systematics and morphology. There is thus extensive material on this subject.

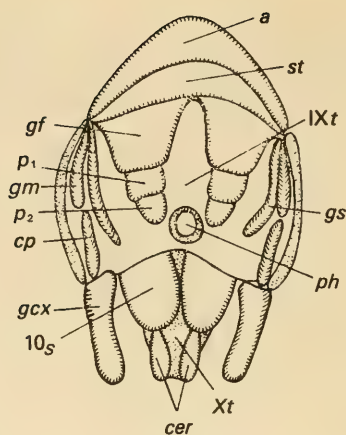


Fig. 22. Structure of the genital appendages in males (after Rubtsov, 1951).

a—Gonacrosternum; *gm*—gonopimeron; *gs*—gonostyle; *gf*—gonofurca; *gcx*—gonocoxite; *cp*—coxopleurite; *p*₁, *p*₂—anterior and posterior parameres; *st*—gonosternite; *ph*—phallus and *cer*—cercus. Roman numerals represent the tergites (*t*) and Arabic numerals the sternites (*s*).

The studies of several investigators show that the ninth genital segment is entirely homologous to the schematized thoracic segment excluding, however, the wing sclerites. Rubtsov (1948, 1951, 1953) recorded that the following individual sclerites, not including the phallus, could be distinguished in the ninth segment of dipterans (Fig. 22). Tergal sclerites take the form of acrotergite and tergite proper (*IXt*). The sternal portion of the segment consists of a single gonacrosternum (*a*), a single sternite proper—gonosternite (*st*) and the bifurcated gonofurcosternite (*gf*), each lobe of which carries the anterior and posterior parameres (*p*₁, *p*₂). Pleural sclerites, four on each side, are represented by gonepisternites extending toward the sternite and gonepimerites (*gm*) located close to the tergite; the third gonopleural sclerite, coxopleurite (*cp*), homologous to trochanter, is articulated to them and the gonocoxite (*gcx*) is articulated to the *cp*. The [cercus] (*cer*) is a homolog of the coxae of the thoracic region. The ninth segment includes the phallus (penis) (*ph*), which is a fairly complex organ with no homolog in the other segments of the insects.

Considering the work done on *Culisetina* mosquitoes, it can be shown conclusively that the main, if not all, sclerite elements are homologous to the typical thoracic segment represented in the structure of the hypopygium (Fig. 23). Only a tergite proper, that is, a

gonotergite, has been distinctly seen among the tergal sclerites of the ninth segment of *Culisetina*, but we have not been able to trace the remnants of the acrotergite.

As in many other *Culicidae*, only the ventrolateral plates of the ninth tergite are heavily sclerotized, while the median portion remains membranous and poorly developed. These lateral sclerotized plates may be called the lobes of the ninth tergite (Fig. 23, IX). Along the distal margin of the lobes of the ninth tergite are rather short setae, the number of which varies widely (Maslov, 1963).

The tenth tergite (in fact, similar to all other structures of the male hypopygium) of *Allotheobaldia longiareolata* has a very pecu-

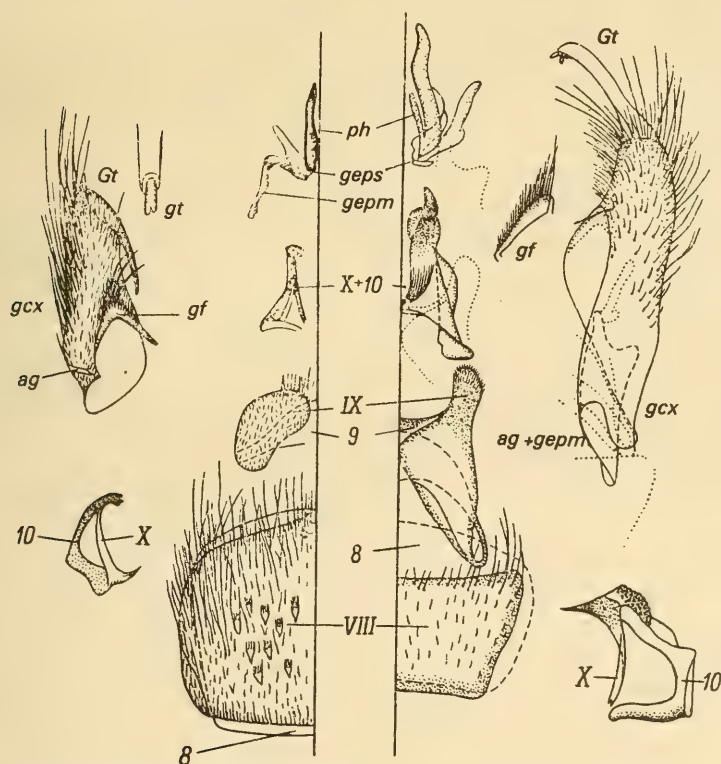


Fig. 23. Disarticulated hypopygium of *Culiseta* (left) and *Allotheobaldia longiareolata* (right).

ag—Apodeme of gonocoxite; gcx—gonocoxite; Gt—gonotelopodite; gf—gonofurca; gepm—gonepimeron; gepts—gonepisternite and gt—gonotelopod appendage. Roman and Arabic numerals indicate, respectively, the tergites and sternites.

liar structure. Here, it consists of two large, greatly elongated, almost
 35 triangular plates (Fig. 23, IX) adjoining each other along the median line. There is a dense growth of short setae on the distal (clavate) portions, the lobes (claspers).

Not all of the sternal sclerites of the ninth segment are fully developed. The gonacrostermite of *Culisetina*, like the acrotergite, is totally indistinguishable and the ninth sternite as such consists of only the ninth sternite proper or the gonosternite (Fig. 23, 9). In *Culiseta*, it is trapezoidal, triangular, semicircular or is a narrow elongated plate articulated with the lobes of the ninth tergite through lateral membranous regions.

The other particularly interesting sternal elements of the ninth segment are the gonofurca (*gf*), a bifurcated sclerite, which is distinctly of sternal origin in *Culiseta*; here, it is in the form of a narrow transverse plate lying posterior to the phallus and continuing into two lobes, lateral bars or lobes joined to the gonocoxites in the form of the basal lobe. The fusion of one gonocoxite with another is hindered by the two lateral lobes of the gonofurca. This does not confirm the statement of Martini (1929-31, p. 70) that, in *Culiseta* as in some other genera (*Megarhinus* and *Uranotaenia*), "zwischen dem Penis und der Mitte des 9. Sternit geht die Basis der einem Valve in der anderen über." We note that the basal lobe in *Aedes* represents simple lobes of the gonocoxite not at all homologous to the basal lobes of *Culiseta*; these are evidently homologous to claspers in *Aedes* and some other Culicidae, as noted by Edwards (1920a). Thus, the claspers of these genera of mosquitoes should be regarded as the lobes of gonofurca, like the lateral lobes in *Culiseta*. Possibly in *Aedes* the base of the clasper corresponds to the gonofurca proper, while one of the remaining parameres of the gonofurca corresponds to the sclerites, which are absent in *Culiseta*.

The lateral lobes of the gonofurca in *Culisetina* vary significantly in their relative dimensions as well as in some other features. Their relative dimensions are best described in the form of a lobe index, that is, the percentage ratio of the height of the lobe to the length of the gonocoxite. The values of this index show the variability of this character in a species while at the same time remaining similar in the different species and even subgenera of *Culiseta*. In the Australian *Culiseta* mosquitoes (subgenus *Neotheobalpia*) and *Austrotheobaldia*, according to Lee (1937) and Dobrotworsky (1954), the lobe index is very high (Figs. 90, 91a; and others) compared to that in all other *Culisetina*, including the subgenus *Climacura* in which it is in fact not more but, on the contrary, lower (39%) than in other *Culiseta* (Figs. 85a and 86a).

Among the other characteristics of the gonofurca, we note the spine-like setae located among the numerous setae on the apex of the lobe. In most Culisetina species, the number of these spine-like setae is 2, but there may be more in some cases. Three setae are often found in *Culiseta annulata annulata*. Three setae are seen far more often on the lateral lobes in *C. inornata*, *C. niveitaeniata* and *C. fumipennis*; the number of setae rises to 5 in *C. annulata subochrea* and *C. silvestris silvestris*, to 7 in *C. melanura*, and to 9 in *C. silvestris amurensis*. A special form of these setae is characteristic of some species. They are acutely, but smoothly curved in *C. glaphyroptera*, (Fig. 66a) and have a characteristic curve in *C. alaskaensis* (Fig. 59a) but, on the contrary, straight, spine-like setae are found in *C. setivalva* (Fig. 80). The gonofurca of *Allotheobaldia longiareolata* differs distinctly from that of Culisetina [sic, *Culiseta*]; in the
 36 former, it takes the form of two completely isolated, hairy, extremely narrow lobes occupying the subapical position on gonocoxites (Figs. 23 and 98, *a* and *b*).

It is more convenient to begin the study of the pleural sclerite not from the gonopleurites themselves but from the homologous extremities of the appendages, which in Culisetina as other Culicidae are not simple but two-segmented appendages. In these cases, the gonocoxite is only the first, basal segment. They are, therefore, called gonopods or gonopodites. The first large segment of the gonopodite, the gonocoxite, as stated above, is homologous to the coxae of the insect leg, while the second may be homologous to the telopod of the lower arthropods and hence with the trochanter and femur of the insect leg. The gonocoxite of Culisetina is in the form of a large elongated, conical appendage articulated at its base with the membranous pleurae, lobe of the ninth tergite and the gonosternite. The structure of the gonocoxite, expressed as the coxite index, that is, the ratio of its length to the thickness at the level of the apodeme (see below), is subject to significant variation.

On its lateral, dorsolateral and ventrolateral surfaces, the gonocoxite is densely covered with long, smooth setae and flat, narrow, leaf-shaped, lanceolate scales. Setae and scales are sparse on the inner surface. From its base arises a fairly long, heavily sclerotized appendage, the apodeme, protruding horizontally inside the conical body of the gonocoxite (Fig. 23). The apodeme represents the point of articulation of the muscles responsible for the movement of the gonocoxite and some other parts of the hypopygium which serves as a lever of articulation with the gonopleural sclerites. The structure of the apodeme in *Allotheobaldia longiareolata* is typical; it (Fig. 23,

ag and *gepm*) is formed as a result of the rotation of its ventro-median surface inside the gonocoxite cone and represents a trough-like broad plate situated under the ventral surface of the gonocoxite and lies parallel to it. As shown by several investigators (Kirkpatrick, 1925; and others), this plate represents not only the apodeme itself, but the results of the fusion of the apodeme with one of the gonopleural sclerites, that is, the gonepimeron (basal plate of the aedeagus, see p. 37).

Among the other features of the gonocoxite is the presence of a fairly well developed apical or subapical appendage in some *Culisetina* which is a simple development of the midventral portion or the median portion of the gonocoxite. This was verified by examining several species. In *Culiseta morsitans* and other members of the subgenus *Culicella*, there are no traces of lobes, not even in the form of hairy thickenings on the distal half of the gonocoxite. In *Culiseta annulata* and *C. bergrothi*, some hairy processes could be distinguished midventrally at the boundary of the median and rear one-third portion of the gonocoxites (Fig. 61*a*). These are more distinctly manifested in *C. incidens* (Fig. 68*b*) in which these setae are additionally characterized by large size and thickness. We know that in *C. alaskaensis* a heavily sclerotized portion, the subapical, is distinctly visible in the apical portion of the gonocoxite. This portion is densely clothed with short, spine-like setae (Fig. 59*a*). In *C. niveitaeniata*, the subapical lobe is large and protrudes, clothed with setae and long, narrow, laminated scales (Fig. 72*a*). The apical lobes attain maximum development in *C. glaphyoptera* (Fig. 66*a*) with a tuft of long laminated scales, resembling the flat subapical lobe of *Culex* mosquitoes.

- 37 A second segment of the gonopod joins the gonocoxite at its apex and is homologous to the telopod of lower arthropods. It is therefore called the gonotelopodite. As in most other mosquitoes, it has a flexed, saber-shaped form. The relative value of the gonotelopod may be expressed in the form of a "gonotelopod index," that is, the ratio in percentage of the length of the gonotelopod to that of the gonocoxite. This factor, which is subject to significant intraspecific variation, remains uniform in different species and subgenera of *Culiseta*. A small appendage (*gt*) (Figs. 23 and 24) is joined to the apex of the gonotelopod in the form of a flattened, slightly bent, ellipsoidal body (*Culiseta morsitans*, *C. fumipennis* and some other *Culicella*). In *C. setivalva*, the appendage is bent and trough-like along its long axis, but preserves the same elliptical form with a rounded free end; however, in *C. bergrothi*, the trough-like append-

age usually has a free end cut straight as a tube cut in half. In *C. annulata*, *C. alaskaensis* and some other members of the subgenus *Culiseta*, the gonotelopod is fairly distinctly bifurcated and this bifurcated portion is very long, giving the impression of two appendages. This is probably the explanation for Liu and Feng's report (1956) that *C. kanayamensis** of northeastern China has two gonotelopod appendages. In *Allotheobaldia longiareolata* this character distinctly differs from that known in *Culisetina* in that the former have not one, but two digitate appendages and they join toward the anterior end of the apical gonotelopod (Fig. 24, 7).

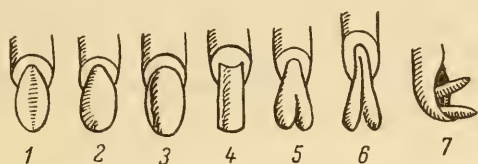


Fig. 24. Types (1-7) of gonotelopod appendages.

Among other gonopleural sclerites, apart from the gonopod, *Culisetina* mosquitoes have paired gonepimerons and gonepisternites forming the aedeagus accessories, that is, the levers associated with the phallus, which carry the ejaculatory duct. Homologs to coxopleural sclerites (corresponding to trochanters) could not be detected in *Culisetina*. The gonepimeron (*gepm*), often called the basal plate of the aedeagus, is in the form of a bent plate (Fig. 23) along with processes with which it joins the apodeme of the gonocoxite and the gonepisternite by joining at its depression. Thus, with this sclerite, muscle attachment is established between the gonocoxites and the copulatory organ, the phallus. As we have noted, the gonepimeron of *Allotheobaldia longiareolata* loses its independence by growing inward with the apodeme of the gonocoxite into a broad plate (Fig. 23, *ag* and *gepm*). One of its processes, as in *Culiseta*, joins the gonepisternites for the protrusion and muscular movements of the gonocoxite and phallus.

The other pleural sclerite of the ninth segment, the gonepisternite (*geps*), also has the form of a plate, but it is situated not parallel, but perpendicular to the longitudinal body axis (Fig. 23). Two processes serve as the attachment for the musculature joint of the gonocoxite with the phallus and they emerge dorsally and ventrolaterally

*These mosquitoes placed by Liu and Feng (1956) among the species *Culiseta kanayamensis* are in fact *C. niveitaeniata* (Maslov, 1963 and 1964a).

as the plate of the gonapisternite. A depression is formed between
 38 these processes. The apical portion of the gonapisternite enters this depression when joined. The plane of the gonapisternite plate serves as a lever on which are fixed the bases of the phallic valves (*ph*). This organ represents the true copulatory organ which consists of two symmetrical valves. In some cases (*Culiseta bergrothi* and members of the subgenus *Culicella*), they are comparatively weakly sclerotized and oval with a somewhat broadened base (Figs. 74*b*, 78*a*, 80; and others). In others (*Culiseta annulata*, *C. alaskaensis*, etc.), the phallic valves are long, heavily sclerotized half-cones (Figs. 74*a*, 59*a*, 61*a*). The ventral and dorsal margins of the phallobase rest on the corresponding extensions of the gonapisternite plate and are joined to each other by the symmetrical valves of the phallus forming a complete conical or oval organ, through which the ejaculatory duct passes.

In *Allotheobaldia longiareolata* (Fig. 23), the gonapisternite is in the form of a semicircular transverse plate with very long dorsolateral processes and the valves of the phallus are very typical. Their base is broadened with a crescentic margin and two parallel processes turned backward. The significantly larger of these occupies the lateral position and the smaller one the median position. These symmetrical, double, comparatively heavily sclerotized valves are joined to each other by a soft membrane forming a tubular structure through which the ejaculatory duct passes.

In Culisetina, the tenth, anal segment is in the form of a cone consisting of symmetrical tergal and sternal sclerites. The tenth tergite, in the form of a very weakly sclerotized narrow plate (Fig. 23, X), occupies the ventral position extending from the apex of the corresponding sternite to the lobe of the ninth tergite and toward the base of the tenth sternite turned ventrally. The sternites of the tenth segment are far more developed than the tergites. They are in the form of sclerotized plates situated dorsally and their bases extend from the dorsal to the ventral surface forming a semicircle. These ventral processes (Fig. 23) lie on the distal margins of the lobes of the ninth tergite forming the broad base of the anal cone. The apical portions of the symmetrical valves of the tenth sternite have 2 to 5 strong teeth. The entirely typical structure of the tenth segment in *Allotheobaldia longiareolata* is in the form of a large, heavily sclerotized structure with distinct tergite and sternite with their distal margins molded into strong, sharp, beak-shaped processes with hemispherical, irregular bases (Fig. 23).

The posterior region of the abdomen in females is of no signifi-

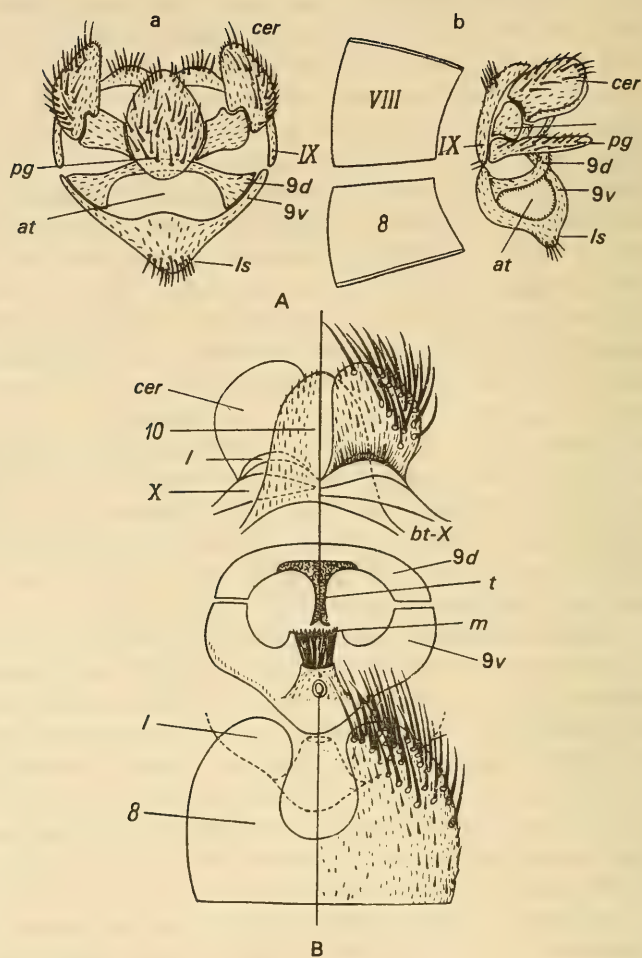
cant systematic interest in most mosquitoes, since there is structural homogeneity in the different species of the same genus and sometimes even in different genera. The eighth segment (Fig. 25) has the same structure as in males. The ninth tergite (Fig. 25, IX) is in the form of a heavily sclerotized narrow arch with two small lobes bearing strong setae, the number of which varies not only in different species but in different members of the same species (Maslov, 1963). For example, in *Culiseta bergrothi*, $M[\text{mean}] = 9.8 \pm 0.33$, range = 6–20 and $n = 66$. Comparison of these variations shows that this feature may be used as an additional character of taxonomic importance, at least in some of the seven species studied (Maslov, 1963, 1964a).

The ninth sternite is in the form of two arches each one curved dorsally (Fig. 25, 9d) and ventrally (Fig. 25, 9v). The latter is sometimes called the sigma (Rees and Onishi, 1951) or ventral bridge 39 (Brolemann, 1919). Sometimes the two arches of the ninth sternite are collectively called the sigma (Kirkpatrick, 1925; Snodgrass, 1959). The ventral arch has a medial projection, a small bridge bearing strong setae, the number of which is extremely variable in each species. The vaginal aperture opens into the wide oval space between the two arches of the ninth sternite, the atrium [at] (gonotreme of Snodgrass, 1959).

The tenth sternite, usually called the postgenital plate (Fig. 25, pg) (Rees and Onishi, 1951; Snodgrass, 1959), bears basal transverse processes (Fig. 25, bt-X) (cowl of Christophers, 1923; Kirkpatrick, 1925; Snodgrass, 1959) through which the sternite articulates with the eighth segment. The tenth tergite is in the form of two small plates (Fig. 25, X) joined with the base of the cercus (Fig. 25, cer). The cercus and plates of the tenth tergite thus limit dorsally the 40 space into which the anus opens; on the ventral surface, it is bound by the tenth sternite.

As in most other morphological features, *Allotheobaldia longiareolata* mosquitoes also sharply differ in this respect from all other members of Culisetina. The greatest difference is in the typical structure of the eighth sternite (Fig. 25B, 8) which has broad lobes with a deep groove between them. Each lobe is covered with strong setae numbering 36.7 ± 0.74 (range = 27–47 and $n = 50$).

The ninth tergite is usually arch-like with slightly distinguished lobes. The structure of the ninth sternite (Fig. 25B, 9d and 9v) is typical. Its dorsal part in the median region has a typical, very distinct, T-shaped sclerotization [t] from the base which divides the atrial cavity in two (Fig. 25B, 9d). The margin of the ventral arch of the ninth sternite restricting entry into the atrium is also heavily



39 Fig. 25. Structure of the posterior end of female *Culiseta* (A) and *Allothoe-baldia longiareolata* (B).

Genitalia of female *Culiseta* are shown in posterior view (a), lateral view (b). at—atrium; 9d and 9v—dorsal and ventral arches of the ninth sternite; ls—islets of ventral arch of the ninth sternite; cer—cercus; l—lobes corresponding to the sclerites; m—median sclerotization of ventral arch; pg—postgenital plate; t—median sclerotization of dorsal arch and bt-X—basal transverse processes of the tenth sternite. Roman numerals indicate tergites and Arabic numerals sternites.

sclerotized along its median portion [*m*] (Fig. 25B, 9*v*). The bridge of the ventral arch is weakly sclerotized and is covered with strong setae numbering 16.4 ± 0.50 (range = 11–21 and $n = 25$). Usually this bridge and its setae are distinctly visible in the groove of the eighth sternite. The tenth tergite and sternite (Fig. 25B, X, 10) are well developed. The tergite has two distinct setaceous lobes with which the cerci are articulated. The sternite (postgenital plate) has distinct basal processes (Fig. 25, 10).

The functioning of the female and male genital during copulation has been studied in detail by Rees and Onishi (1951) in *Culiseta inornata* and is evidently similar in all species of *Culiseta*. This has also been confirmed in *C. annulata subochrea* from the Syr Darya River basin and *C. bergrothi* (Fig. 26) near Khabarovsk.

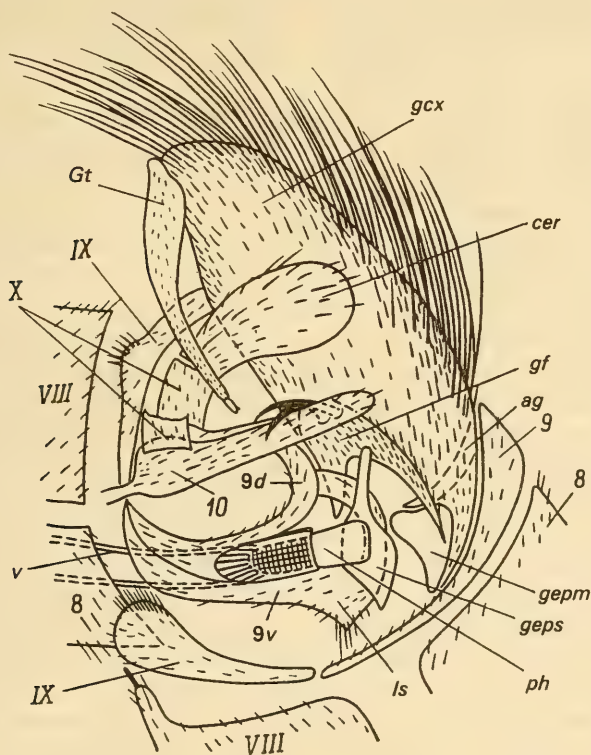


Fig. 26. Position of genital appendages in *Culiseta bergrothi* during copulation.

v—Female vagina. Remaining as in Figs. 23 and 25.

MORPHOLOGY OF PRE-IMAGINAL STAGES

Oviposition

Little has been studied about the oviposition and structure of ova in mosquitoes of the subtribe Culisetina. We know that in the genus *Culiseta*, the members of the subgenera *Culiseta* s. str., *Climacura* 41 and *Neotheobaldia* and the typical genera *Austrotheobaldia* and *Allotheobaldia* lay eggs in the form of small rafts, while the members of the subgenus *Culicella* do so singly. The Australian species *C. inconspicua*, which oviposits in the form of rafts, is an exception. According to Frohne (1953), the egg rafts of *Culiseta impatiens* are flat and rectangular, while those of *C. alaskaensis* are triangular or elongated in the form of a small boat with one end pointed and the other bluntly rounded. The rafts of *C. melanura* are rounded or oval; according to Dobrotworsky (1954), *C. inconspicua* is similar in this regard.

According to some investigators, the number of eggs in a raft (Table 2) varies significantly. This has been analyzed in great detail by Maslov (1963) on the basis of three Central Asian and one Far Eastern species. Our investigations showed that, depending on the number of eggs laid, the form of the egg raft may be different in the same species: rectangular, pointed, rounded, oval, otherwise. Thus, the form of the egg raft cannot be regarded as a reliable taxonomic feature. This is also true for the eggs themselves as their dimensions may vary widely from 0.6 to 1.2 mm in length with a maximum thickness of 0.25–0.4 mm. They are usually elongated or oval with a very broad base and tapering apex (Fig. 27). The ratio of the length 42 of the egg to its maximum thickness, called the egg index, shows the extent of elongation of the egg. In some instances, there is a difference in the amount of egg curvature (Fig. 27) and in the nature of pigmentation. While describing the eggs of two North American species, Frohne (1953) showed that *C. alaskaensis* had great egg curvature and a pattern of 4 dark rings alternating with 3 light ones; the eggs of *C. impatiens*, on the other hand, are comparatively straight and have a medial light brown zone marginally fringed by a very dark brown base and apex. However, as Frohne noted, such pigmentation was preserved only in developing eggs with growing larvae, but was not seen in empty egg shells. Dobrotworsky (1954) reported uniform coloration (silvery eggs with black base) in three Australian members of the subgenus *Neotheobaldia*: *Culiseta hilli*, *C. frenchi* and *C. victoriensis*. These differ distinctly from each other

in the egg index: 2.8–3.2 in *C. victoriensis*, 3.4–3.5 in *C. frenchi* and 4.3 in *C. hilli*. In the eggs of *C. inconspicua*, unlike those of the former three species, Dobrotworsky (1954) recorded uniform black coloration and an index of 4.0. Roughly similar characteristics (uniform dark coloration and index about 4.0) were described by Chamberlain for the eggs of the American *C. melanura*.

41 Table 2. Number of eggs in rafts of some species of the subtribe Culisetina

Species	No.	Range	Mean $\pm$ SE
<i>Culiseta alaskaensis alaskaensis</i> , Alaska (from the data of W.C. Frohne, 1954)*	58	75–325	184.3 $\pm$ 7.2
<i>C. alaskaensis indica</i> , Syr Darya River basin (author's material)	27	98–277	175.0 $\pm$ 9.3
<i>C. annulata annulata</i> , England (Marshall, 1938)	—	100–300	200 —
<i>C. annulata subochrea</i> , Syr Darya River basin (author's material)	22	22–256	114.8 $\pm$ 12.5
<i>C. bergrothi</i> (author's material) from:	237	54–341	172.9 $\pm$ 1.35
Amgun River basin	12	171–279	219.0 $\pm$ 8.9
Khabarovsk town zone	207	54–341	172.6 $\pm$ 3.5
Kamchatka	4	198–291	237.5 $\pm$ 24.0
Bikin River basin	14	58–207	121.0 $\pm$ 11.9
<i>C. impatiens</i> , Alaska (Frohne, 1953)*	158	26–182	91.7 $\pm$ 2.3
<i>C. inornata</i> , Nebraska, USA:			
Edmunds	—	148–292	204 —
Newkirk	—	—	145 —
<i>C. silvestris silvestris</i> , Ukraine (Val'kh, 1957)	—	47–201	— —
<i>C. inconspicua</i> , Australia (Dobrotworsky, 1954)	1	217	— —
<i>C. melanura</i> , Georgia, USA (after Chamberlain)	11	85–102	100 —
<i>C. antipodea</i> , Australia (Dobrotworsky, 1962)	1	102	— —
<i>C. frenchi</i> , Australia (Dobrotworsky, 1954)	—	—	90 —
<i>C. hilli</i> , Australia (Dobrotworsky, 1954)	—	up to 60	— —
<i>C. victoriensis</i> , Australia (Dobrotworsky, 1954)	—	up to 60	— —
<i>Allotheobaldia longiareolata</i> , Syr Darya River basin (author's material)	33	34–291	157.5 $\pm$ 11.1
<i>Austrotheobaldia littleri</i> , Australia (Dobrotworsky, 1954)	—	up to 60	— —

*The author (A.M.) conducted the biometric calculations based on these data.

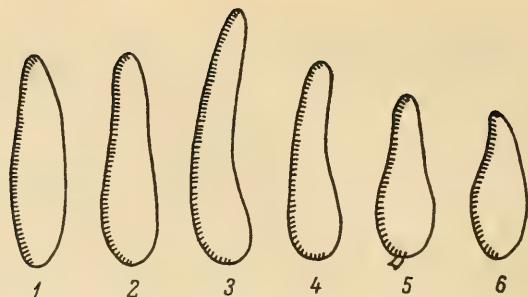


Fig. 27. Types of Culisetina eggs.

1—Moderately long, symmetrically ellipsoidal; 2—Moderately long, symmetrical tapering; 3—Long and asymmetrical; 4—Moderately long and asymmetrical; 5—Short and symmetrical with stem; 6—Asymmetrical.

The author's investigations of ovipositions in Far Eastern *C. bergrothi* and Central Asian *C. alaskaensis indica*, *C. annulata subochrea* and *Allotheobaldia longiareolata* show a wide range of variation in the pigmentation of developing eggs and in the values of the egg index. It has been noticed that the eggs at different sites in an egg raft (along the fringes and in the middle) may have extremely varying indices: for example, in *C. bergrothi* the values vary from 3.0 to 4.2. Pigmentation varies in the eggs according to the stages of larval development. Not all of these egg characteristics are presently useful as taxonomic features.

Larva

Body dimensions and color. The fourth instar larvae of Culisetina mosquitoes attain a length of 15 mm or more. As in many other insects, the larval growth of mosquitoes does not proceed evenly. The heavily sclerotized body portions increase in dimensions only during molting, as long as the integument has not hardened. The dimensions of other body portions with soft integument initially increase (after molting) due to the lengthening of the cuticle within a period of 6 to 16 hours. Later, growth ceases for some time and proper growth, typified by an even increase in dimensions, begins on the second day after molting and extends throughout the entire stage until the next molting. This property precludes the use of body length as a determining feature for dimensions, since the larvae of the fourth instar, a day after molting, differ sharply from the larvae of the same fourth stage surviving for 3 or 4 days. Moreover, as in

43 adult mosquitoes, comparative morphological studies, especially those showing geographic variations, usually do not deal with fresh, but with preserved material; during fixation, the soft integument undergoes change at the joints while the heavily sclerotized body parts preserve their absolute and relative dimensions.

These factors necessitated the adoption of such characteristics as the length of head (from the collar to the foremargin), maximum width of head and length of respiratory siphon measured along the dorsal surface (Fig. 48) to describe the size and its variation in larvae. Special investigations (Maslov, 1952, 1963) showed that the absolute body dimensions of all species of *Culisetina* studied, varied widely depending on the topographic and geographic conditions, meteorological factors, feeding regime, and so on.

The color of *Culisetina* larvae does not vary much. The thorax and abdominal segments are covered by a soft, weakly sclerotized integument which is usually pale or yellowish or of light brown shades depending on the amount of melanin in the endocuticle; this pigment is evidently unique to the larvae of *Culisetina*. However, as shown by several investigators (Kuznetsov, 1951; Monchadskii, 1936, 1951, and others; Shvanvich, 1949; Wigglesworth, 1933a), the color of such weakly sclerotized body portions is to some extent due to the pigmentation of the fat body of the intestine and its contents seen through the integument and to the pigment of plant origin adhering to the insect body. In the pale larvae (mostly of the subgenus *Culicella*) and in many other members of the family Culicidae, the thorax and abdominal segments are comparatively darker dorsally than ventrally. Other body portions (head with its appendages and siphon) have dark coloration which varies in different species from yellowish to almost black.

By arranging color in a decreasing order of intensity, 9 classes of a variation scale have been defined to describe separately the sclerotized body portions of the head and siphon of larvae. Special studies of larval color in relation to their geographic and other distribution conditions (Maslov, 1952, 1963) revealed a broad range of variation in all larvae studied in this respect. In *Allotheobaldia longiareolata*, the head is particularly darker, as reported by several investigators (Brolemann, 1919; Kirkpatrick, 1925; Monchadskii, 1936, 1951).

On the other hand, the head and siphon of species of the subgenus *Culicella* are extremely pale, similar in this respect to larvae of most Palearctic species of *Culex* as described by Martini (1929-31), Monchadskii (1936, 1951) and Peus (1935). There is an interesting report by Dobrotworsky (1954) on this subject stating

that the larvae and pupae of Australian *Culiseta* (subgenus *Neotheobaldia*) inhabiting subsoil water reservoirs are devoid of any pigment and are milky-white in color.

Different patterns, in the form of comparatively dark dorsal spots due to heavy sclerotization in the regions of articulation of the oral muscles, have been recorded in comparatively pale specimens, independent of the specific origin. This pattern is most distinct in different species of the subgenus *Culicella* and in the light *Culiseta alaskaensis indica* and *C. annulata subochrea*.

- 44 The typical form of the head pattern of *Culiseta* larvae is shown in (Fig. 28). A single round spot (*a*) located almost medially on the frontal shield can be called the central sincipital spot (Monchadskii, 1951, p. 15) representing the articulation zone of the epipharyngeal musculature. Posterior to it is a similar single, larger, posterior sincipital spot (*b*), representing the articulation zone of the inner retractor of the labrum. Along the sides of the frontal sclerite are situated three lateral paired spots; the anterior lateral spots (*c*) at the margin of the frontal sclerite in front of the epicranial sutures representing the articulation zone of the outer retractor of the labrum; the median and posterior lateral spots (*d* and *e*) together with the anterior spot are situated in a straight line directed posteriorly from the median lateral rim of the frontal sclerite toward the epicranial suture. The latter two pairs of spots represent portions of a muscle articulation, i.e., the dilators pharyngealis. Apart from these spots, portions of the freely articulated frontal setae (5, 6 and 7), especially the inner one (5), the posterolateral regions of the frontal sclerite and the posterior fringe of the head beyond the boundary of the frontal sclerite up to the ocular seta usually are comparatively darkly pigmented. The hard portions of the posterolateral region of the head serve as the articulation zone of the abductor muscles of the maxillae and mandibles.

In Culisetina, we find larvae with strong pigmentation additionally on the thorax and sometimes even on the abdominal segments. It is invariably well developed on the thorax around the bases of prominent setae, especially the group of pleural setae 9-12 (Figs. 46, 47). Here, the heavy sclerotization of the integument also serves as the attachment of corresponding muscle tendons.

Chaetotaxy. Small epicuticular microtrichia fairly densely cover the whole cuticular surface of different body regions, but are distinctly seen especially on the antenna, siphon and dorsal plate. In the fourth instar larvae of *Culiseta silvestris amurensis*, the antennal microtrichia cover the entire antenna. On the proximal and distal

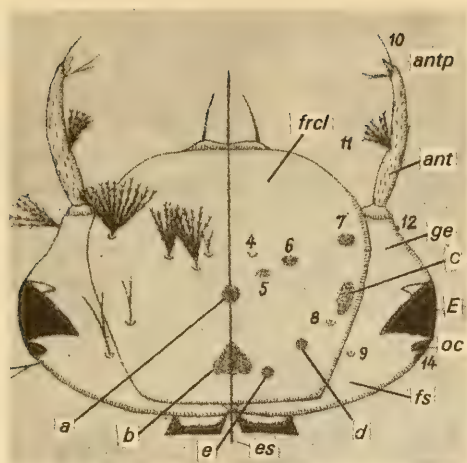


Fig. 28. Structure of head in larvae (dorsal view). To the left are shown the setae and to the right are shown their numbers.

ant—antenna; *antp*—antennal process; *a, b, c, d, e*—portions of main muscle attachment shown by sclerotization on frontal sclerite; *E*—compound faceted eye; *ecs*—epicranial suture; *frcl*—frontoclypeus; *fs*—frontal suture; *ge*—gena; *oc*—ocellus.

[1, 2, 3—clypeal setae; 1a₂, 3—outer and inner lateral clypeal setae; 4—posterior clypeal seta; 5, 6, 7—inner, median and outer frontal setae; 8—sincipital seta; 9—trans-sutural seta; 10, 11—antennal setae; 12—subantennal seta; 14—ocular seta.]

one-third of the antenna, they are relatively short (20–30 μ) and in the median one-third portion noticeably longer (up to 40–50 μ). In the fourth instar larvae of *C. silvestris silvestris*, right at the base of the antennae, the microtrichia are relatively short and thick (8 $\times$ 30–40 μ) and later, before deviating from the antennal setae, they become longer and thinner (5–6 $\times$ 40–60 μ), while the distal ones become shortened and thickened (8–10 $\times$ 15–20 μ); thus, they descend slightly beyond the middle of the separated apical portion of the antenna. In the fourth instar larvae of *C. morsitans*, the microtrichia are long (30–40–50 μ) at the antennal base (up to one-tenth of its length), even more elongated (about 60 μ) distally, up to one-fourth of the antennal length; later, they became gradually and continuously shorter (about 8–10–12 μ) and appear thus in the region of the antennal seta.

45 Microtrichia as such have not been detected on the dorsal plate [saddle] of the species of the subgenus *Culiseta* s. str. studied in this respect (*C. bergrothi*, *C. annulata*, *C. alaskaensis*, *C. glaphyoptera*, *C. niveitaeniata*, *C. incidens* and *C. inornata*). The microscopic

examination of the saddle shows characteristic arcuate or broken beam-like thickenings 25–50 μ or more in length, arranged in irregular rows parallel to the longitudinal axis of the anal segment. Similar thickenings are seen in the central one-third length of the saddle in the fourth instar larvae of *C. morsitans* (Fig. 29A) or along the extreme ventral surface in the fourth instar larvae of *C. silvestris* (Fig. 29B). Later, very tiny denticles (1–5 μ) are seen initially in the distal region on these thickenings and these gradually diminish in number, but elongate to 25–30 μ in *C. morsitans* and up to 10–12 μ in *C. silvestris* (Fig. 29).

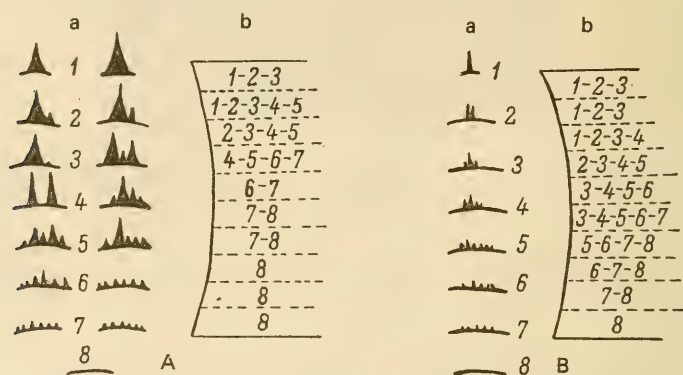


Fig. 29. Microscopic structure of saddle in *Culiseta morsitans* (A) and *C. silvestris amurensis* (B). a—types of denticles and b—arrangement of denticles (according to types) on saddle surface, (anterior-posterior regions).

On the saddle of the first instar larva of *Allotheobaldia longiareolata*, in its posterior half, we find minute, sparsely arranged, paired denticles scattered without a definite arrangement, set on beam-like thickenings of the cuticle and slightly denser along the dorsal margin (Fig. 30). In the second instar larva, the spine formation begins even in the mid-posterior region, that is, in the posterior one-third of the saddle where minute denticles are seen initially; later triple and paired denticles also arise; finally, the anterodorsal region of the dorsal plate is covered almost exclusively by single, short (6–10 μ) or long (15–20 μ) setae (Fig. 30). The saddle of the third and fourth instar larvae of *A. longiareolata* almost all along its length has a smooth cuticle and only its anterodorsal margin is covered with fairly numerous, long (up to 150–180 μ in L^4)* and

* L^4 = fourth instar larva [Editor].

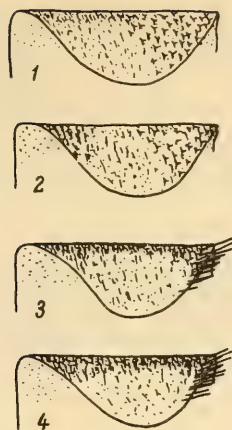


Fig. 30. Microscopic structure of saddle in the larvae of all four instars of *Allothelobaldia longiareolata*.

short ($5-10\ \mu$ or longer in L^4) spines which are typical of this species (Fig. 30).

Isolated, mobile, true setae lie in their own cavities, joined to the cuticle, indicating their origin from special hypodermal trichogen cells; are especially numerous and characteristic in larvae. Here, they often play a significant role as systematic features, although varying widely as noticed by various investigators (Martini, 1929-31; Monchadskii, 1936, 1951; Rempel, 1950; and others). Most setae on the head, thorax and abdominal segments belong to this category (Fig. 31).

Using some examples, we can demonstrate the interrelations and common origin of different types of setae in Culisetina larvae. *Culiseta bergrothi* larvae show a gradual transition from the scaly structure of the comb with a typical tooth of the siphon ridge (Fig. 32a) and the whole range of transitions from typically broad multiple teeth (Fig. 32b) to typically long setae; this can be seen in one specimen of the same species. Similar transitions are also seen in other larvae of the subgenus *Culiseta* s. str., but in representatives of the subgenus *Culicella* we see gradual transitions in the comb from a multitude of wide serrations to solitary strong spinules or rudimentary, barely noticeable, spinules, differing very little from the microtrichia.

The functional importance of setae and other spiny elements vary as greatly as their forms. Most of these setae, located on the

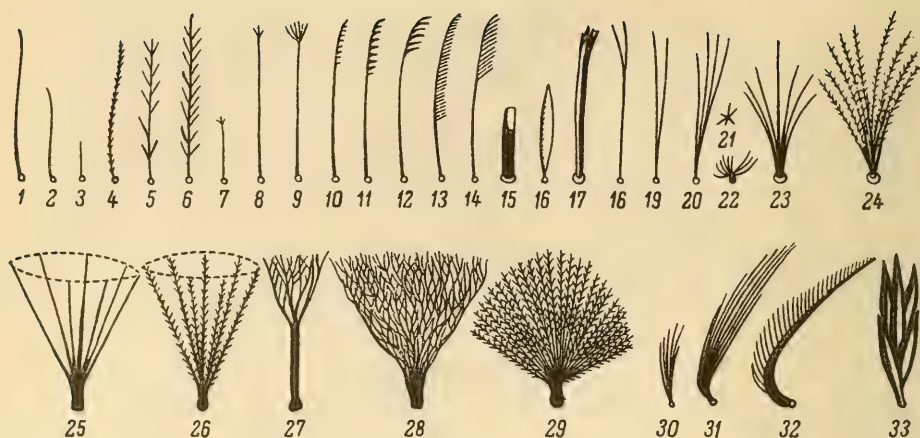


Fig. 31. Types of larval setae.

1—simple and long; 2—simple and short; 3—simple and rudimentary; 4—simple, long and pubescent; 5—simple, long and slightly plumose; 6—simple, long and plumose; 7—simple, short and laciniated; 8—simple, long and laciniated; 9—simple, long and verticillated; 10—simple, long and slightly serrated; 11—simple, long and serrated; 12–14—simple, long and cristated; 15—dolabriform; 16—simple, leaf-shaped; 17—simple, furcated; 18—simple, long and bifurcated; 19—paired and long; 20—slightly branched; 21—branched and rudimentary; 22—branched and short; 23—branched, long and smooth; 24—branched, long and pubescent; 25—cone-shaped and simple; 26—cone-shaped and pubescent; 27—scopiform; 28—dendritic; 29—flabellate tuft of setae; 30—fin-shaped and short; 31—fin-shaped and long; 32—plumose; 33—multiple, leaf-shaped.

head, thorax and abdominal segments in different directions, also act as receptor organs and are fairly extensive sensitive areas in the body of the larva.

Among the other functions of setae are their help in swimming (setae of the fin [paddle] on the anal segment). They also support the body on the water surface (palmate and some other larval setae). Of great interest are the hook-shaped variation and the articulation of the setae found near the rear valves of the stigmal plate in *Culiseta fumipennis*. The hook-shaped setae enable the larvae to hold on to the aquatic vegetation during prolonged retention under water; the larvae breathe the oxygen exhaled by the leaves. A similar phenomenon is known although to a lesser extent in *C. morsitans* and some other larvae (Monchadskii, 1936, 1937; Wesenberg-Lund, 1920–21).

The diverse types of setae, teeth and spines found on the labrum,

maxillae, clypeus and other organs forming complex mouth parts are extremely important to the larval feeding process. These are described below:

Head and its appendages: The head capsule is invariably somewhat flattened in the dorsoventral direction. This flattening and with it the relative width of the head, varies in different species of Culisetina. To describe the forms of the larval head, it is convenient to use the head index, which represents the ratio of the maximum width of the head to its length measured along the midline from the occiput to the anterior fringe, without the collar and the clypeus. The lowest value of head index is found in the larvae of *Allotheobaldia longiareolata*, in which it averages 1.17 ± 0.003 with a variation range of 1.1 to 1.5. In the mosquito larvae of the subgenus *Culiseta* s. str. the value of head index exceeds 1.25 but is under 1.5, while it exceeds 1.5 in the larvae of the subgenus *Culicella*. Furthermore, wide ranges of variation have been noted (Maslov, 1963) in the value of the head index in every species. We will not analyze this variation (Maslov, 1952, 1961a) but we note that individual variations of the head index within a species or subspecies are evidently caused by the same factors responsible for subgeneric and generic differences, that is, by the nature and conditions of larval feeding (Maslov, 1961a, 1963, 1964a).

The larvae or immature stages can be distinguished in each species by the lower value of the head index which increases from one stage to another.

Sclerites. The frontal shield stands out on the dorsal surface (Fig. 28, left), also called the frontal sclerite or the frontal clypeus (Bekker, 1938a, 1938b; Marshall, 1938; Matheson, 1944). The last of these names is the most appropriate, since a part of the clypeus fused with the frontal sclerite actually forms the major portion of the dorsal plate of the head.

The frontoclypeal plate is in the form of a rectangle, fairly swollen with rounded corners demarcated from the other portions of the head by the frontal suture (Fig. 28, *fs*). The clypeus is separated from the frontal plate by an epistomal suture and it forms the anterior portion of the head. The clypeus carries a pair of strong setae turned forward. The lateral cephalic surfaces form the lateral plates or genae (*ge*), called the epicranial plates in non-Russian literature, separated dorsally from the frontal shield by the frontal suture. Posteriorly, the symmetrical genae, adjoining each other, form the epicranial suture (*es*). Below, the genal plates adjoin the gular plate (Fig. 33) and are set off from it by the subgenal sutures (*sgs*) which are well distinguished in all Culisetina apart from the first instar



47 Fig. 32. Transitional structural forms of scaly denticles and dentate setae in the larvae of *Culiseta bergrothi*.

a—scaly denticles and b—dentate setae.

larvae. The anteroventral margins of the genae adjoin the heavily sclerotized tentorial arms carrying the mandibular bases. The head plate anteriorly adjoins the base of the submentum (*smt*). The lateral margins of the gular plate have different forms in different groups of Culisetina depending on the configuration of sutures surrounding it. In species of the subgenus *Culiseta* s. str., they are straight and extend parallel to the midline of the body. At some distance from the anterior rim, a heavily sclerotized labrum and prementum join it (Fig. 33, *lm*). In the larvae of the subgenus *Culicella*, the gular sutures are relatively very short and sharply arched away from the midline of the body. In *Allotheobaldia longiareolata*, the gular sutures are bent concave towards the midline of the body. In larvae of Culisetina along the midline on the gular plate, the median gular suture extending backward up to the occipital foramen (*oc*), could be clearly distinguished. The occipital foramen in Culisetina larvae is relatively narrow and is surrounded by the heavily sclerotized occipital plate, the collar, in the form of two semicircles set off from each other along the midline on the dorsal side corresponding to the epicranial suture and on the ventral surface

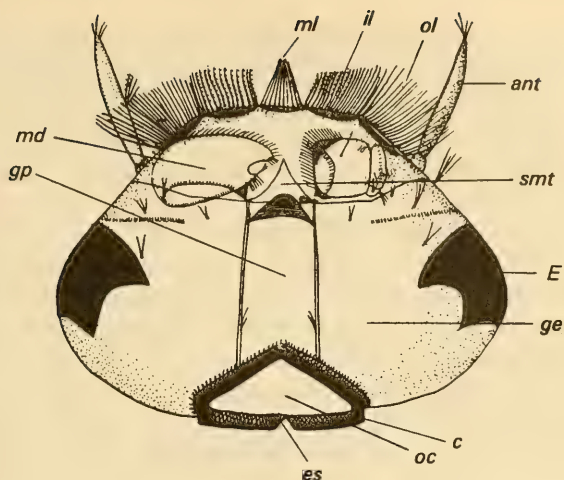


Fig. 33. Structure of head of fourth instar larvae (ventral view).

il—inner lobe of labrum; *gp*—gular plate; *md*—mandible; *ol*—outer lobe of labrum; *oc*—occipital foramen; *smt*—submentum; *fs*—frontal suture; *es*—epistomal suture; *fr*—frontoclypeal plate; *ml*—middle lobe labrum; *lm*—outer lobe of labrum.

along the median gular suture. The variations of relative collar length with age described for *Anopheles* larvae of different stages do not apply to Culisetina and to many other Culicidae.

Eyes. In larvae of all stages we find simple eyes which are preserved in the pupae and adult mosquitoes. In adults they do not function as they are covered by scales. Compound faceted eyes are found (although very poorly developed) even in the second instar larvae; they are distinctly visible in the third instar larvae and attain complete development only in the larvae of the fourth stage. The compound eyes are crescent-shaped (Fig. 28, *E*) and set on the genae at the widest portion of the head, descending dorsally and ventrally. The simple eyes in the form of small, also crescent-shaped spots (at least in the fourth instar larvae), are set immediately posterior to the compound eyes. In juvenile larvae, the shape of the simple eyes is more rounded, especially in the first instar larvae.

Chaetotaxy of head (Figs. 28 and 33): The complete set of setae consists of 21 pairs on the head visible dorsally and ventrally without any segmentation of their individual parts (Marshall, 1938). In Culisetina mosquitoes, as in all other genera, not all the setae are

developed to the same extent and some are absent. Here the synonyms have been ignored and the basic terminology of Monchadskii (1951) has been adopted. This has been modified according to Marshall (1938) with other changes and additions mostly concerning setae, on the ventral portion of the head, which were not considered by Monchadskii.

Strong, clypeal setae, slightly curved inward, are present on the extreme anterior region of the head, on the lateral projections of the clypeus (seta 1). The lateral clypeal seta (1a) seen in the larvae of *Anopheles* and some species of *Aedes* and other genera is absent in *Culisetina* larvae. Here the inner and outer setae of the clypeus (2 and 3) are also absent; these play a major role in the systematics of *Anopheles*. Posterior clypeal setae (Fig. 28, 4) are usually small, weakly branched and distinctly shifted posteriorly; these are seen in *Culisetina* only slightly anterior to the inner frontal setae. In *Culisetina* the group of frontal setae are the best developed: inner (5), median (6) and outer (7). They are arranged in or form straight rows with their bases. These rows are arranged at an obtuse angle to each other toward the antennae (Fig. 28) or the bases of these setae on the right and left sides form symmetrical triangles or the lines of the bases of these setae form an almost regular, perpendicular, longitudinal axis of the head. The relative disposition of the frontal setae and the posterior setae on the clypeus are, in relation to the frontal setae, extensively used in systematics. Particularly after the special investigations of Peus (1930a), this characteristic has been regarded as a vital feature in distinguishing *Culiseta annulata subochrea* from *C. annulata annulata*: in the larvae of the latter, the bases of the posterior setae of the clypeus do not descend medially beyond the bases of the inner frontal setae while in *C. annulata subochrea* they are distinctly shifted toward the center of the longitudinal line of the head.

Frontal and postclypeal setae in different species of *Culisetina* are characterized by their relative size and extent of branching. In the larvae of *Allotheobaldia longiareolata* and the species of the subgenus *Culiseta* s. str., the length of all frontal setae is less (Fig. 28) and rarely exceeds one-half of that of the head. It is different in species of the subgenera *Culicella* and *Climacura* in which the median frontal setae stand out sharply by their exceptional length; in an overwhelming majority of cases, this length exceeds the length
50 of the head (Fig. 34). This feature, expressed in the form of an index of the median frontal seta, the ratio of the length of seta 6 to that of the head (expressed as a percentage), is an excellent diagnostic criterion.

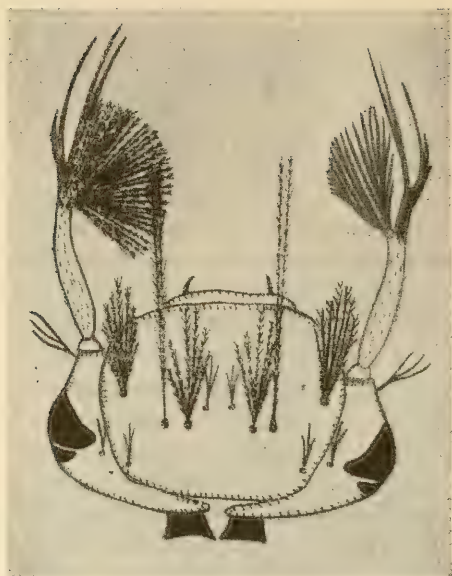
ion for identifying the subgenera and some specific taxa. The length of the median frontal seta in *Culicella* and *Climacura* is directly correlated to such characteristics as the head index, length of the antenna (antennal index), number of branches of the antennal seta and finally, to the filtration type of feeding to which we refer later. The frontal setae belong to following setal types: branched, long, plumose (Fig. 31, 24), simple, long (Fig. 31, 1), paired, long or short (Fig. 31, 19); and so on. Simple and paired setae are found among the fourth instar larvae of *Allotheobaldia longiareolata* and occasionally among other groups and, in the latter instances, this is relevant only to the median frontal setae. In general, the median frontal setae have less branching. The fourth instar larvae of *Culiseta bergrothi* have the most branches on the median frontal setae among all the fourth instar larvae studied in this respect and have about 14 branches with the mean $= 9.2 \pm 0.043$. In some instances, among the members of the subgenus *Culicella*, the median frontal setae have a homogeneous nature, invariably two-branched (*C. silvestris amurensis* and *C. morsitans dyari*). The branching of other frontal setae has changed greatly and varies from an average of 5.5 for the outer frontal setae (more branched) in *C. fumipennis* to 11.4 in *C. bergrothi*, with a variation range of 2–16 branches. The inner frontal setae have an average of 2.7 (*C. morsitans morsitans*) to 9.54 (*C. bergrothi*) branches with a variation range of 2–13 branches.

The number of branches of the frontal setae has been used in systematics, sometimes as a formula of frontal setae* in which the numbers of branches of the median (numerator) and inner (denominator) setae are expressed as a fraction, that is, 6/5. However, because of their significant variation, this character can be used in systematics only with utmost care and that too only as an additional feature along with the other, more important characters.

In the more juvenile larval stages, the number of branches of the frontal and of all other setae decreases from stage to stage and, in the first instar larvae, the cephalic setae, with some rare exceptions, are simple.

Other dorsal setae of the head, the sincipital setae (8), trans-sutural (9) and ocular (14) are monotypic in all Culisetina: they are simple, two- or three-branched, short and thin (Fig. 28). The sincipital setae are close to the posterior margin, from the flanks of the frontal plate. Trans-sutural setae are set on the genae close to the

*According to Marshall (1938), frontal setae formula; according to Martini (1929–31)—Stirnhaarformel.



49 Fig. 34. Head of the larva of subgenus *Culicella* (*C. silvestris amurensis*).

sincipital setae. The ocular setae are placed immediately posterior to the simple eyes. They are best called supraorbital setae to distinguish them from infraorbital setae located posterior to the eyes on the ventral surface of the head (15).

Antennal setae (10 and 11) will be discussed later with the antenna. We will now describe the last pair of setae visible on top (12) which Monchadskii, in the second edition (1951) of his review, called the antennal root hair. In the first edition (1936) he, like many other foreign scientists, called them sub-antennal. Marshall (1938) called them the basal setae as distinguished from the subbasal setae (13), only visible ventrally. They are, in fact, close to the antennal bases, almost on the extreme anterior margin of the lateral surfaces of the genae (Fig. 28, 12). We prefer then to give them the topographic name, upper anterior genal setae and the setae located below
 51 them on the ventral surface of the head (13), the lower anterior genal setae. The upper anterior genal setae of *Culisetina* mosquitoes are similar to the frontal setae, that is, pubescent-flabellate with significant branching.

Setae on the ventral surface of the head, including the mandibular (16 and 19), which we will discuss while studying the maxillae, are very poorly developed in *Culisetina*. They are simple or two- or

three-branched, often rudimentary. Among such setae, apart from the lower anterior buccal (13) and infraorbital (15) setae, are the anterior (17) and posterior (18) transmaxillary (basal maxillary setae and post-maxillary setae according to Marshall) and gular setae (20) (submental setae according to Marshall).

Antennae: Antennae (Fig. 28, *ant*) are set on the symmetrical anterior projections of the genal plates and are freely articulated with the head. The mobility of antennae and their form, relative length, type of setae and so on, are correlated to the structures of the mouth parts and other features which depend on the method of feeding. The relative length of the antennae is most conveniently expressed in the form of an antennal index, that is, the percentage ratio of the length of the antenna (without apical setae and appendages) to the length of the head measured by the ordinary method. In typical filter-feeding scrapers, the antennae are poorly mobile, weakly flexed, of uniform thickness all along their length and only slightly tapering apically. They are relatively short, with an index not exceeding 50%. They are particularly short in *Allotheobaldia longiareolata* in which the antennal index is only $31.2 \pm 0.18\%$ with a variation of 20–40%. On the other hand, in the typical filter feeders, represented by species of the subgenera *Culicella* (Fig. 34) and *Climacura* (Figs. 85b and 86b), the antennae are long with an index of or exceeding 100%, greatly flexed with a distinctly variable thickness in the proximal region up to the point of articulation of the setae (11) and with narrow, distal portions.

The antennal surface of Culisetina is usually clothed with tiny spinules—microtrichia—the abundance and disposition of which may vary even within a given species or range; this is apparent from details of individual developmental conditions. In most cases, the spinules most densely cover the antennal base or its center; in other cases, they are scattered fairly uniformly all along the surface or are concentrated at the apex. In the fourth instar larvae of *Culiseta bergrothi* and some other species of the subgenus *Culiseta* s. str. we often found antennae completely devoid of spinules. In the larvae of *Culicella* and *Climacura*, there are generally many more antennal spinules than in other groups of Culisetina, while they are absent in *Allotheobaldia longiareolata*.

Sensory setae are found at the apex of the antenna (Fig. 35). They are essentially monotypic in all Culicidae. The sensory setae include digitate processes (Fig. 35, *10*) often in the form of setae and the dolabriform process (Fig. 35 *d*), called the hyaline process by Marshall (1938). The three terminal antennal setae (Fig. 35, *10* and *10a*)

are set in two groups: one seta occupies the extreme apical position along with the processes and the other two which could be called subterminal setae (10a) are some distance from the apex.

The hairy tuft on the antennal tip called the antennal tuft (11) is as variable as any other cephalic structure. It is set almost in the center of the antenna close to the base (subgenus *Culiseta* s. str.); in *Allotheobaldia longiareolata* it is nearly in the center but slightly toward the apex. In *Culicella*, it is one-third the distance from the apex or closer to it. The antennal tuft is not a single seta with branches arising from a common base, but a bunch of individual, sometimes densely flagellate setae. The tuft setae in many cases are plumose (Fig. 31). Depending on the type of larval feeding, the relative length and number of setae in the tuft vary (Maslov, 1952, 1961a). In *Allotheobaldia longiareolata*, the tuft is extremely short and hardly noticeable at the tip of a darkly pigmented antenna consisting of 2-4 weak setae. In the larvae of the subgenus *Culiseta* s. str., which feed mainly by scraping vegetation, there is a whole range of transitions from a comparatively weak tuft in *Culiseta niveitaeniata* (5.1 ± 0.187 branches with a variation range of 3-8) to a well developed one in *C. bergrothi*. In the latter, the number of setae varies between 5 and 19 with a mean value of 12.4 ± 0.06 . In typical filter feeders of the subgenus *Culicella*, the number of tuft setae increases to 16-30 as in *C. morsitans* (mean = 21.9 ± 0.19) and even to 20-40 as in *C. silvestris amurensis* (mean = 31.3 ± 0.423). They are even more numerous in the American *Culiseta melanura*.

The antennae have many important functions. They carry mechanical receptors and thus discharge the function of sensory organs. Moreover, the antenna as a whole, and especially its hairy tuft, help the larvae direct the water current during their feeding by the filtration method.

The structural elements of the antennae in the larvae of younger stages are more homogeneous. Depending on the extent of metamorphosis, the differences between the antennae of filter feeders and scraping feeders become increasingly distinct. Thus, while the antennal tuft is single branched in almost all the first instar larvae, those of the second instar are distinctly branched and especially so the larvae of the third; branching is most fully developed in the fully grown larvae.

Mouth parts: The mouth parts of mosquito larvae are the orthopterous type. Some parts vary significantly, especially the structures of the labrum, depending on the nature of feeding.

Many investigations (Cook, 1949; Wesenberg-Lund, 1920-21)

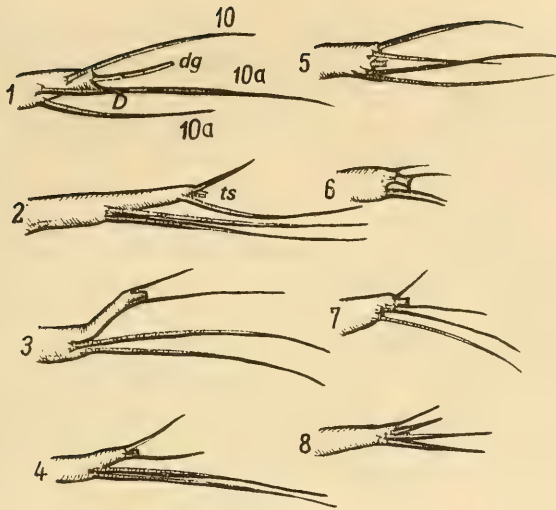


Fig. 35. Structure and types (1-8) of apical antennal appendages.

d—Dolabriform appendage; *dg*—digitate appendage; *ts*—terminal spine;
10—terminal spinule (*tsp*); *10a*—subterminal spinule (*stsp*).

have been conducted on the structure and functioning of the mouth apparatus of *Anopheles* larvae and certain species of *Culex* and *Aedes*. In a special publication describing a detailed study of the mouth parts of *Culiseta incidens* larvae (Cook, 1949), there is an excellent description of the muscle system of the labrum, labium and pharynx but morphological study of the maxillae is absent. It is therefore necessary to describe in some detail the individual mouth parts of Culisetina larvae since among Culisetina we find distinct differences of larval feeding such as filter feeding and typical scraping of vegetation. Our description may not, however, be complete.

Although the mouth parts of the various larvae differ significantly in structure depending on the nature of feeding, feeding by Culisetina larvae is not strictly confined to one method. Typical filter feeders (subgenus *Culicella*) are capable of scraping vegetation as typical periphytophages such as *Allotheobaldia longiareolata* are capable of filter feeding on plankton. Consequently, even the morphological structures of these larvae preserve versatility to some extent which is variously manifest in the different members.

The labrum is in the form of a complex system of freely moving setae and filaments forming a single, unpaired median and two lateral lobes or flabellae (or tufts; flabellum of foreign authors). The

main function of this apparatus, consisting of several hundreds (thousands) of filaments, in all Culisetina, is to direct the water currents toward the oral cavity. The skeletal sclerites of unpaired and paired lobes of the labrum are freely articulated through a system of levers with the thickened anterior and lateral margins of the frontal sclerite, with the clypeal processes and with the epipharynx beneath the labrum which in turn also bears numerous setae.

The structure, working mechanisms and functional importance of all the elements of the labrum described by Bekker (1938a) for the larvae of *Anopheles* and by Shalaby (1957a, 1957b, 1957c) for some larvae of Culicinae correspond in principle in most aspects to the larvae of Culisetina. The hairy structures, the labrum and epipharynx in different Culisetina as demonstrated by Wesenberg-Lund (1920-21), are not identical in terms of the feeding mechanism. Filter feeders of the subgenus *Culicella* feeding on plankton have flabellae set far apart from each other (Fig. 37, 5) and separated by the broad base of the unpaired fibrous lobe of the distomedian palatum. Each lateral lobe (flabellum) in turn is fairly sharply subdivided into outer and inner portions. The outer portion in the form of a tuft of numerous filaments is turned sideways at an obtuse angle to the longitudinal body axis; each filament of this outer portion, however, is slightly arcuately curved forward. The inner portion of the flabellum also consists of numerous filaments, but here both the filaments and the tuft are set in the same forward direction with a flexure toward the longitudinal body axis. There is often a transitional hairy zone between the outer and inner tufts of the lateral lobe; in other instances, the tufts are distinctly separated from each other. Corresponding to the broad base of the lateral lobes of the labrum, changes are seen in the main system of levers responsible for
 54 its articulation. These changes effect elongation of the humeral-arcus of the postmedian epipharyngeal process and arcus of the longitudinal lever and an elongation of the clitellum and other levers compared to those present in *Anopheles* larvae (Bekker, 1938a). The musculature also undergoes a change: the outer retractors of the labrum and antennal musculature and of the mandibles (see below) and some other muscles situated in the lateral portions of the head (Fig. 39, b) are well developed as a result of which the cephalic index of *Culicella* larvae is higher than of phytophagous forms.

In the larvae of the subgenus *Culiseta* s. str., which feed by scraping vegetation, the hairy portion of the labrum has a different structure (Fig. 37, 1 and 2). The lateral lobes here are not as widely set apart and, correspondingly, the median unpaired lobe, that is, the

distomedian palatum, has a noticeably narrower base. Here the separation of each lateral lobe into two tufts is not distinct. The outer filaments of the flabellum, slightly flexed, arching inward, are turned anteriorly and laterally. They are somewhat thickened and straightened near the mid-portion and are directed anteriorly. Close to the body midline, the filaments on the lateral lobe are even thicker, with a typical S-shape bend and usually have tiny denticles at their apices (Fig. 36). These denticles form a characteristic crest or scraper. It is this scraper which is used to scrape the periphyton. A far less visible S-shaped flexure and crenation are also found on the inner filaments of the flabellum in the larvae of subgenus *Culicella*; these larvae are capable of not only filter feeding on plankton, but feeding by scraping the periphyton. The thick S-shaped filaments, intensely developed on the lateral lobes of the labrum of the larvae of *Allotheobaldia longiareolata*, are particularly interesting. Capable of predatory feeding (and cannibalism), the larvae of *A. longiareolata* without any specialized adaptations as in the predatory larvae of the subfamily Culicinae (*Toxorhynchites*, *Lutzia* and some others), hold their quarry not only with the thick S-shaped filaments of the inner lobe, but with the entire flabellum of the labrum.

Based on a comparison of all the structural forms of labrum encountered in Culisetina larvae, five groups were defined (Fig. 37 and Table 3).

In the larvae of *A. longiareolata*, periphytophages with obligatory predation, the labrum has specific features which have been described above (Fig. 37, 0).

The epipharynx joins the ventral surface of the base of the labrum along the midline restricting the oral cavity above. In Culisetina larvae, the epipharynx is in the form of a system of spines, setae and filaments turned downward toward the oral cavity. They are set on symmetrical, sclerotized lever beams joined with the labral levers. Paired and unpaired muscles, the opposite ends of which are

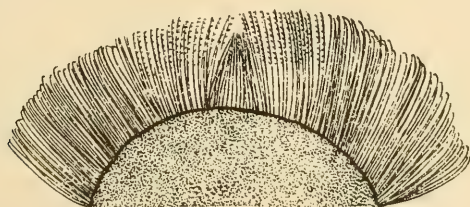
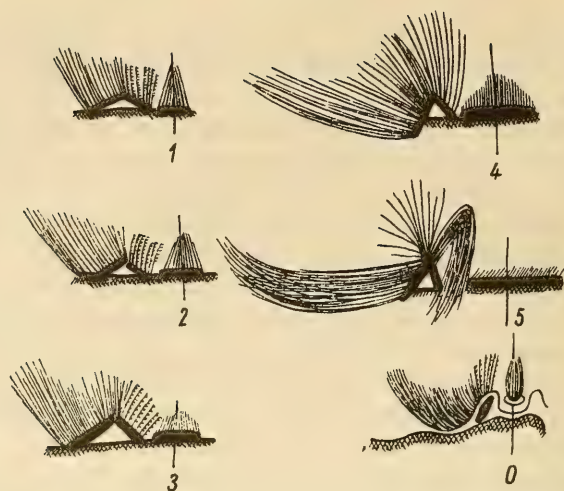


Fig. 36. S-shaped serrated filaments of the labrum in the 4th instar larva of *Culiseta niveitaeniata*.



54 Fig. 37. Groups (1 to 5) of labral structure in different *Culisetina*.

joined inside with the frontal plate near spot *a*, are articulated to the sclerotized epipharyngeal levers and represent one of the points of heavy sclerotization of the frontal plate (Fig. 28). As pointed out by Bekker (1938a) and Monchadskii (1951), the function of the epipharynx is two-fold: it holds the food entering the oral cavity and, with the parts of the labrum, helps to direct the water current toward the oral cavity. Unlike *Anopheles*, filaments predominate among the epipharyngeal processes in larvae of *Culisetina*. Furthermore, they are longer, thinner and more numerous in the filter feeders and shorter, thicker and fewer in scrapers. In the latter, various types of spines (cultriform, dolabriform, serrated, others, Fig. 31) and setae are well developed along with the filaments.

The mandibles (Fig. 38) mark the boundary of the oral cavity on the dorsolateral surface. The mandibles consist of two valves: the flatter ventral and bulging dorsally. These transit into each other and form rounded anterior and outer margins. Along the posterior margin, the dorsal and ventral mandibular plates do not come into contact with each other but form a fairly broad longitudinal tube leading to the maxillary cavity, thus coming into contact with the oral cavity. The margin of the mandibular plate limiting this opening is heavily sclerotized.

The mandibles bear different types of teeth, spines, processes and setae on their surface. On the inner margin two large spines stand out prominently turning toward the symmetrical jaw; they are

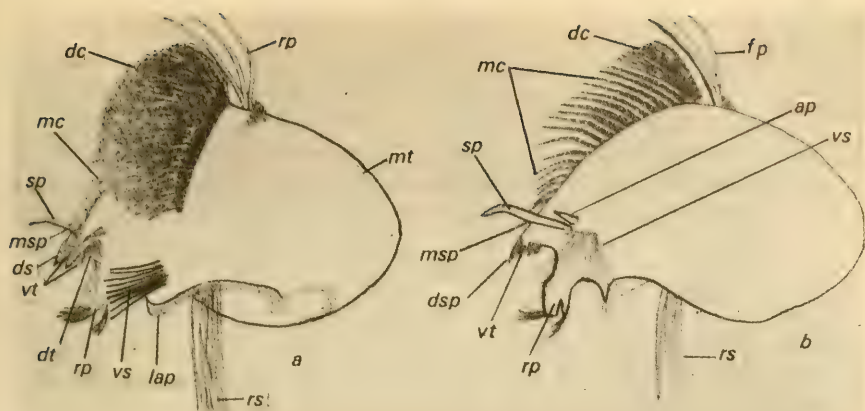


Fig. 38. Schematic depiction of the mandibles of larvae adapted to universal type of feeding (*Culiseta bergrothi*).

a—dorsal view; *b*—ventral view; *ap*—additional process; *ds*—dorsal setae; *dc*—dorsal crest; *dt*—dorsal teeth; *dsp*—dorsal spine; *fp*—falciform process; *mc*—marginal crest; *msp*—marginal spine; *mt*—microtrichia; *lap*—labial articular process; *rp*—rostriform process; *rs*—rear setae; *sp*—saber-shaped process; *vs*—ventral setae; *vt*—ventral teeth.

called the marginal (Fig. 38, *msp*) and dorsal (Fig. 38, *dsp*) spines. On the dorsal surface more teeth (Fig. 38, *dt*) are found along with the dorsal spines; the *dt* vary in number and size depending on the type of feeding (Maslov, 1961a, 1963).

56 On the dorsal mandibular surface, apart from large teeth, there are usually some small denticles varying in number and not considered while describing the mandibular structures. On the dorsal surface close to the posterior margin there is a group of long dorsal seta (Fig. 38, *ds*) and a row of fairly long, numerous setae [filaments] extends from the anterior to the posterior margin. These filaments are set on a ribbed fold on the dorsal crest (Fig. 38, *dc*) (mandibular brush of Shalaby, 1957a, 1957b and 1957c and lateral comb of Mitchell [Mitchell], 1906). The relative growth of the dorsal crest may be expressed in the form of an index, that is, the ratio of the length of the largest seta to the maximum length of the maxilla measured from the outer to the inner margin including the dorsal and ventral teeth. The value of this index expressed as a percentage differs in relation to the type of feeding (Maslov, 1961a, 1963).

Outside the ribbed base of the marginal crest on the anterior margin of the mandible there are three freely moving falciform processes turned anteriorly and inward (lateral bristles of Shalaby,

1957a, 1957b, 1957c) (Fig. 38). The base of these processes is set off by the wedge-shaped process of the mandibular dorsal wall. Usually, in the larvae of filter feeders, these falciform processes are relatively long and thin, while they are short and strong in the periphytophages. Anterior to the marginal spine, along the foremargin, there is a regular row of fairly long, rigid filaments occupying the entire anterior-inner margin of the labrum almost up to the falciform processes, also called the marginal crest (Fig. 38, *mc*) [marginal comb of Mitchel [Mitchell] (1906) or dorsal setae of Bekker (1938b)]. Depending on the nature of feeding, the marginal comb filaments may be firm and spiny (in periphytophages, Figs. 38, *mc*; 40) or in the form of extremely short, soft hairs (in filter feeders, Fig. 40, and in *Allotheobaldia longiareolata*, Fig. 40, *0*); they are set on a cone-shaped, elevated anterior margin of the mandible.

On the ventral surface, at the same site as the group of dorsal teeth, we find the ventral teeth (Fig. 38, *vt*); together these form the complex of mandibular biting elements. These are well developed in the periphytophages and in the predatory *A. longiareolata*. Slightly away toward the center on the ventral surface is the mobile saber-shaped process (pectinate hair of Shalaby, 1957a, 1957b, 1957c) (Fig. 38, *sp*) and along with it a second additional process (Fig. 38, *ap*) which is sometimes absent. The saber-shaped process projects far beyond the antero-inner maxillary margin and is distinctly seen in *Culisetina* (with the exception of *A. longiareolata*) not only from the ventral, but also from the dorsal sides (Fig. 38, *a*). Sometimes it is extremely long, smooth and pointed, while in other cases it is shorter and bears a rough or sharply crenated inner surface. The latter is usually seen among the periphytophages and in the universal *Culiseta bergrothi* larvae feeding other than by filtration (Maslov, 1961a).

On the ventral surface, posterior to the base of the saber-shaped and additional processes, there is a group of ventral setae [filaments] (Fig. 38, *vs*). On the posterior margin, almost medially there is a third group of setae [filaments] (rear setae, Fig. 38, *rs*) called spines by Bekker (1938b) in *Anopheles*. These propel the food into the pharynx. Their function is also similar in *Culisetina* and they could thus be called pharyngeal setae.

Below the complex of biting elements occupying the innermost position of the posterior margin of the mandibles, there is a relatively weakly sclerotized rostriform process (membranous process of Shalaby, 1957a, 1957b, 1957c, Fig. 38, *rp*) with two branches—
57 anterior and posterior—each carrying a tuft of spicules turned toward the biting complex.

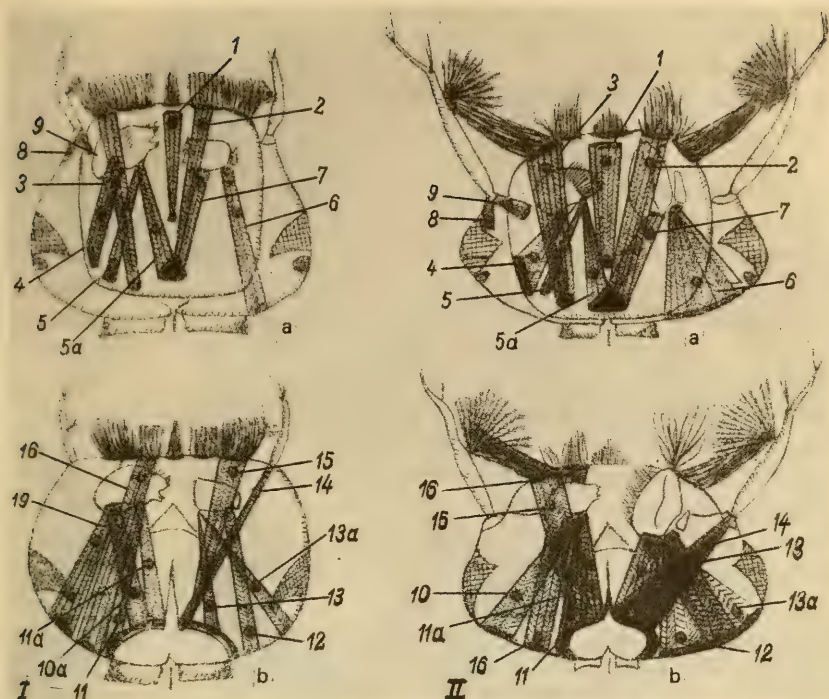


Fig. 39. Arrangement of the main cephalic muscles in the larvae of scrapers (I) and filter feeders (II).

a—muscles attached to the dorsal sclerites of the head; *b*—muscles attached to the ventral sclerites of the head; 1—unpaired muscle (retractor) of epipharynx; 2—inner retractor of labrum; 3—outer retractor of labrum; 4—dorsal abductor muscles of maxilla; 5 and 5*a*—dorsal abductor muscle of maxilla; 6—dorsal abductor muscle of mandible; 7—dorsal abductor muscle of mandible; 8—dorsal abductor muscle of antenna; 9—dorsal adductor muscle of antenna; 10 and 10*a*—ventral abductor muscles of maxilla; 11 and 11*a*—ventral adductor muscles of maxilla; 12—ventral abductor muscle of mandible; 13 and 13*a*—ventral adductor muscles of mandibles; 14—ventral muscle of antenna; 15—ventral muscle of the outer lobe of labrum; 16—ventral muscle of the inner lobe of labrum.

The mandible is articulated with the maxillae through a ventrally articulated tooth of the genal plate (Fig. 41, *lmx*) and directly with the mandibular articular process situated on the posterior margin (Fig. 38, *lap*) outside the rostriform process. It is formed by the joining of the dorsal and ventral surfaces and restricts the tube leading to the maxillary cavity. Another articular process in the form of a lobe on the dorsal wall joins the maxilla with the articular maxil-

lary tooth of the buccal sclerite (Fig. 41, *lmx*). Finally, the sclerotized margin of the ventral wall serves as articulation with the paired branch of the V-shaped trabeculae and, through it, directly with the hypopharynx.

The functional importance of the main elements of the mandible in *Anopheles* larvae has been studied in detail by Bekker (1938b).
 58 The functioning of this part of the mouth apparatus in Culisetina larvae is generally similar. The filaments of the marginal crest and falciform and saber-shaped processes brush the filaments of the labral lobes passing through the crest, thus removing the food particles adhering to the labral filaments. The filaments of the dorsal crest with those of the hypopharynx surround the oral cavity preventing food particles from receding with the water. The teeth of the inner margin are turned not toward the symmetrical jaw, but somewhat downward and anteriorly; they do not masticate the food but help in breaking the food bolus by lightly tapping on the hypopharynx, which serves as an ingenious anvil. The tufts of the pharyngeal filaments push the food bolus forward into the pharynx thus helping the pharyngeal musculature to swallow the food. The maxillae of the larvae of periphytophages also help in scraping the periphyton. With the labral S-shaped filaments, this function is discharged by the teeth and falciform and saber-shaped processes and the rigid setae of the marginal crest of the mandible.

The diverse functions of the mandible necessitate a complex muscular system (Fig. 39). The adductor and abductor muscles of the mandible proper are among the main muscles responsible for maxillary articulation. The tendons of these muscles are joined with the outer margin of the maxilla body and with the base of the rostriform process. The movements of the mandibles are also controlled by the abductor and adductor muscles of the paired branch of the V-shaped trabeculae and by the musculature of synchronously functioning maxillae with which, as noted, the mandibles are freely articulated. The opposite tendons of all these muscles are attached from within to the heavily sclerotized sections of the dorsal plates of the head (Fig. 39, *a*). Fixed from within on the ventral plates of the head is another set of mandibular muscles, in particular the flexors toward the hypopharynx and many others (Fig. 39, *b*).

Based on the nature of the individual mandibular components present in the *Culiseta* [Culisetina] larvae, the mandibles could be grouped into 5 classes analogous to the labrum (Fig. 40, Table 3).

The maxillae are freely articulated with the antero-ventral margin of the genae. They are also joined to the labium and mandibles

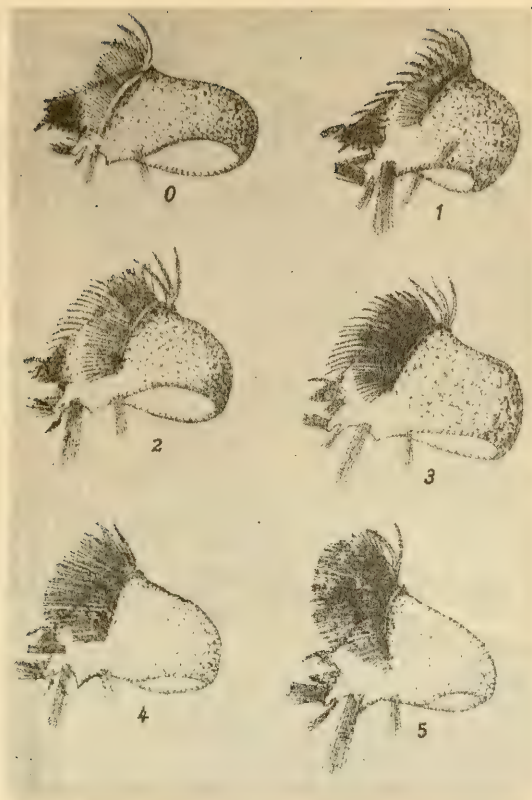


Fig. 40. Classes (0 to 5) of mandibular structure in the fourth instar larvae of various *Culisetina*.

and restrict the oral cavity laterally and partly from below. The maxilla (Fig. 41) consists of small stipes with which are articulated the mandibular lobe and the palp. The stipes (Fig. 41, *st*) is in the form of a highly sclerotized triangular formation of the maxilla bearing a small but distinctly perceptible, 2-3-branched seta which may be called the stipal seta and, continuing the enumeration of Marshall and other scientists, is assigned the number 21. With the stipes, the maxilla is joined with the articular tooth of the gena (Fig. 41, *atg*) with which the mandible is also joined. The maxillary body or the maxillary lobe (Fig. 41, *lmx*) is formed as a result of the fusing of outer (galea) and inner (lacinia) lobes of the primitive orthopteran maxilla. In *Culisetina* larvae, depending on the nature of feeding, the maxillary body may be flattened, rectangular and parallel or flattened, ellipsoidal and pointed toward the apex or any inter-

Table 3. Features of the main types of oral apparatus in larvae

Functional features of mouth parts	Class of structure	Labrum	Mandible	Maxilla	Musculature (important characteristic muscles)	Larvae
Feeding through periphyton scraping	1	Outer and inner lobes not separated. S-shaped filaments numerous and thick with distinct crenation at apex. Single tuft of palatum with a narrow base.	Number of large dorsal teeth exceeds 5. Saber-shaped processes sharply crenated. Marginal crest consists of few, short, strong spines. Index of dorsal crest less than 15%.	Body quadrate (index 0.9 to 1.0) or slightly extended in the transverse direction. Apical tuft of filaments absent. Index of marginal crest less than 30%.	Adductor and abductor muscles of maxillae and muscles of inner lobe of labrum most intensely developed. Muscles of mandibles, outer lobe of labrum and antenna poorly developed (Fig. 39, I)	<i>Culiseta annulata annulata</i> , <i>C. annulata</i> , <i>C. subochrea</i> , <i>C. alaskaensis</i> , <i>C. alaskaensis</i> .
" "	2	Outer and inner lobes poorly separated. S-shaped filaments moderately thick with distinct crenation. Single tuft of palatum with a narrow base.	Number of large dorsal teeth 4-5. Saber-shaped processes with tiny denticles. Marginal crest consists of few, moderately long, strong filaments. Index of dorsal crest 15-20%. Index of marginal crest less than 15%.	Body quadrate (index 1.0) often with a faintly rounded apex. Apical tuft absent. Index of marginal crest 30-40%.	Same	<i>Culiseta annulata subochrea</i> , <i>C. alaskaensis</i> , <i>C. alaskaensis</i> , <i>C. alaskaensis indica</i> , <i>C. bergrothi</i> , <i>C. glaphyoptera</i> , <i>C. impatiens</i> , <i>C. incidens</i> , <i>C. inornata</i> , <i>C. niveitarsata</i> .
Mixed (filter and scraping) feeding	3	Outer and inner lobes set off by a transitory zone.	Number of large dorsal teeth 2-3 (4). Saber-shaped	Body slightly extended longitudinally; index	All the above muscles relatively well developed.	<i>Culiseta alaskaensis indica</i> , <i>C. bergrothi</i> .

C. glaphyrophtera,
C. impatiens,
C. inornata,
C. niveitaeniata.

up to 1.2. Apical
 tuft bears no more
 than 10 poorly
 developed
 filaments. Its
 index is less than
 50%. Index of
 marginal crest
 40-50%.

processes with
 very tiny denticles
 or without
 indentation.
 Marginal crest
 consists of 12-15
 thin, moderately
 long filaments.
 Its index is 15-20%.
 Index of dorsal
 crest 20-25%.

Filaments of the
 outer lobe set
 forward and
 slightly sideways.
 S-shaped filaments
 thin with a weak
 apical crenation.
 Single tuft of pala-
 tum with a moder-
 ately broad base.

Culiseta bergrothi,
C. niveitaeniata,
C. morsitans,
C. silvestris
silvestris,
C. silvestris
amurensis.

Same
 Body oval with an
 index of 1.3 or
 more. Apical tuft
 consists of 15-25
 filaments. Its
 index is 50-100%.
 Index of marginal
 crest 50-60%.

Number of large
 dorsal teeth 1-3.
 Saber-shaped
 process without
 indentation.
 Marginal crest
 consists of 16-20
 long setaceous
 filaments. Its
 index exceeds
 20%. Index of
 dorsal crest
 25-30%.

Outer and inner
 lobes separated.
 Filaments of outer
 lobe turned
 distinctly sideways.
 Transitional zone
 present between
 outer and inner
 filaments. S-shaped
 filaments poorly
 developed or absent
 Single tuft of
 palatum with a
 broad base.

Filter-feeding of
 plankton

5

Outer and inner
 lobes sharply set off
 without transitory
 zone. Filaments of
 outer lobe turned
 sharply sideways.
 S-shaped filaments
 absent. Single tuft
 of palatum with a
 very broad base.

Number of less
 prominent, large,
 dorsal teeth 0-3.
 Saber-shaped
 process simple.
 Marginal crest
 consists of short
 setaceous fila-
 ments. Index of
 dorsal crest ex-
 ceeds 30%.

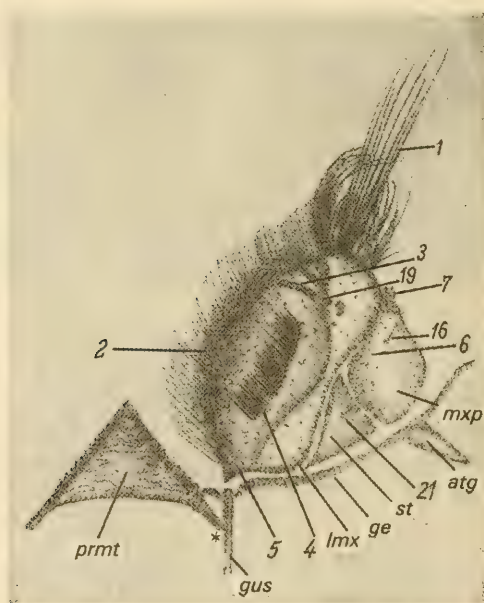
Body oval-ovoid
 with index
 exceeding 1.3.
 Apical tuft
 intensely devel-
 oped and consists
 of over 25 fila-
 ments. Its index
 exceeds 100%
 Index of mar-
 ginal crest ex-
 ceeds 60%.

Adductor and
 abductor muscles
 of mandibles,
 muscles of outer
 lobe of labrum
 and antenna
 gradually
 strengthened.
 Maxillary
 muscles some-
 what weak (Fig.
 39, II).

Most of the members
 of the genus
Culiseta (sub-
 genus *Culicella*,
Climacura and
Neothoeobaldia;
Austrotheobaldia
littleri, *Theomyia*
fraseri.

mediary form. In no instance is the ventral surface flat. From the outer margin, the maxillary body gradually rises in the form of a Shuster's lean-to up to the center or further toward the inner margin and is interrupted immediately thereafter forming a fairly distinct median rib (Fig. 41). The surface of the maxillary lobe adjoining the inner margin is thus noticeably below its outer surface. The median rib in some cases extends almost longitudinally while in other cases, it is curved toward the outer margin or shows other features. In *Allotheobaldia longiareolata* larvae, the ventral wall of the maxillary lobe forms a typical upturned flap (Fig. 42, 0).

The characteristics of the form of the maxillary lobe are expressed as a maxillary index, that is, the ratio of its length to width. In typical periphytophages, the value of this index is about one or even less, that is, the maxillary lobe is quadratic in form or slightly broad-



59 Fig. 41. Structure of maxillae of larvae with universal type of feeding.

atg—articular maxillary tooth of gena; ge—gena; gus—gular suture; lmx—lobe (body) of maxilla with filaments; mxp—maxillary palp; prmt—prementum (asterisk points to the articulation of prementum with gular suture); st—stipes; 1—apical tuft of filaments; 2—marginal crest; 3—digitate appendages; 4—ventral crest; 5—labial articular process; 6—ventral median rib; 7—terminal sensory appendage of palp.

ened transversely*. Particularly interesting are the *A. longiareolata* larvae in which the maxillary index may vary from 0.7 to 1.1–1.2. If, in larvae with mixed feeding, filtration further develops, the nature of the maxillary body also undergoes a change along with other transformations. It is extended longitudinally (the index becomes 60 1.1 to 1.3 or more) and acquires an elliptical form with a pointed apex. The extreme type of such a form is seen in the filter feeder larvae of the subgenus *Culicella* (Fig. 42, 4 and 5). The boundary of the inner and posterior maxillary margins forms a sclerotized dentate maxillary process (Fig. 41, 5).

The maxillary body bears numerous filaments and setae among which the apical tuft is very interesting (Fig. 41). The apical tuft is absent in the extreme periphytophages (Fig. 42, 1) with the exception of *A. longiareolata*, in which this tuft bears an original form and is turned not anteriorly but inward (Fig. 42, 0). In larvae with mixed feeding we found successive development of the apical tuft bearing from a few to 15 or more filaments. Correspondingly, the apical tuft index (percentage ratio of the length of the longest filament to the maxillary length) changes from 25–30 to 70% or more. In specific filter feeders, the larvae of the subgenus *Culicella*, the apical tuft has an index exceeding 100% and bears over 25 filaments.

There is a marginal crest along the inner margin of the maxilla, mostly at the dorsal but to a lesser extent on the ventral surface (Fig. 41). It consists of numerous setae [filaments] and spines of diverse forms set in various directions, as in *Anopheles* larvae (Bekker, 1938b). The percentage ratio of the length of the longest filament of the crest to the maxillary length (marginal comb index) varies in relation to the nature of feeding. The index does not exceed 40–45% in periphytophages (Fig. 42, 1). It increases to 50–60% in larvae with mixed feeding (Fig. 42, 3 and 4) and attains a maximum of over 60% in the specific filter feeders (Fig. 42, 5). The larvae of *Allotheobaldia longiareolata* bear only a hairy tuft posterior to the center of the inner margin with sparse, very short filaments at the base instead of the full marginal crest covering the entire inside and descending on to the anterior margin of the maxilla (Fig. 42, 0).

A group of filaments in the form of a ventral crest is seen on the inner ventral surface of the jaw in some species of *Culiseta* (Figs. 41 and 42). In other cases, the crest is absent, but there is a fairly well developed ventral tuft of filaments on the median rib (Fig. 42) or

*In the more primitive *Anopheles* larvae, the maxillary index is even less, only 0.6 to 0.7.

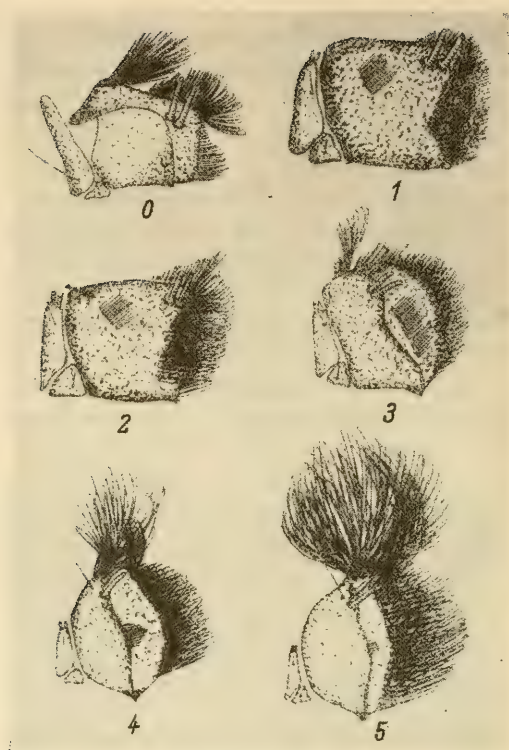


Fig. 42. Classes (0 to 5) of maxillary structure in the 4th instar larvae of *Culisetina*.

lateral to it. A large single or more rarely two- or three-branched mandibular seta 19 (maxillary seta of Marshall, 1938) stands out prominently. Its maximum length and strength is in *Allotheobaldia longiareolata*.

- 61 Among the other structural elements of the maxillary lobe are the two well developed digitate appendages set alongside each other on the ventral median rib, almost at the very apex, in all *Culiseta* (Fig. 41). In *A. longiareolata*, these digitate appendages are situated not on the median rib, but on the inner surface close to the maxillary base (Fig. 42, 0).

The maxillary palp (Fig. 41, *mxp*) is well developed in the periphytophages and larvae with mixed feeding (Fig. 42, 1-3) but not so in the filter feeders (Fig. 42, 5). Apically it bears one, two or more, often three terminal sensory setae, and usually an indistinguishable

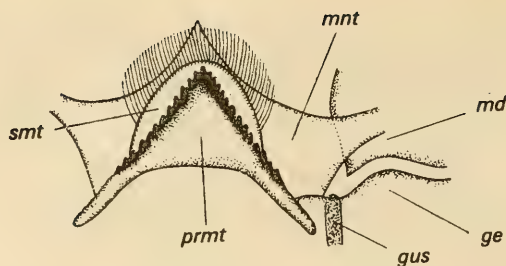
palp seta 16 (palp hair of Marshall, 1938). These setae are long and stout only in *A. longiareolata* (Fig. 42, 0).

Here too, as in the labrum and mandibles, five classes can be established by comparing the structures described above (Fig. 42 and Table 3).

As in other cases, the typical maxillary structure of *A. longiareolata* demands the placement of this type of maxilla in a special zero class (Fig. 42, 0).

The functional importance of the maxillae in Culisetina larvae is not identical. The marginal crests turned toward each other on the symmetrical jaws represent in all cases an apparatus to hold the food particles in the oral cavity. In the filter-feeding method, the dense marginal crests help to catch and strain tiny food particles from the water as in *Anopheles* larvae (Bekker, 1938b). With the apical tuft and other oral elements described above, these help in generating and in controlling the direction of the water during filter-feeding. The importance of the maxillae in the filtration process is confirmed by their comparatively good development in larvae of the subgenus *Culicella* in which, additionally, they have a high degree of mobility, unlike the weakly mobile maxillae of periphytophages. Corresponding to this activity, the maxillary musculature is also strengthened as we see in a comparison of this structure in different *Culiseta* (Fig. 39).

The labium forms the floor of the oral cavity in its anterior half. In larvae of *Culiseta*, as in most other mosquitoes, it is relatively poorly developed and consists of three plates set one over another. The outer weakly sclerotized triangular plate, the submentum (Fig. 43, *smt*), is joined to the anterior margin of the cranium and becomes an element of the ventral wall of the head capsule. The apex of the submentum is covered with numerous, fairly long and arcuate plumose setae (Fig. 31). The second part is a triangular plate, the mentum (Fig. 43, *mnt*), which is more deeply set and projects slightly forward beyond the apex of the submentum. There are small teeth and one large apical tooth on the lateral margins of the mentum. Sclerotization of the mentum is similarly insignificant although more distinct than on the outer plate. Finally, the prementum is set even more deeply (Fig. 43, *prmt*) and forms the bottom of the oral cavity. Unlike the other labial plates, the prementum represents a heavily sclerotized, crenated triangular plate, which is translucent and shows structures lying below and hence distinctly identifiable when the larval head is seen ventrally (Figs. 33 and 43, *prmt*). The two bases of its lateral margins are greatly extended



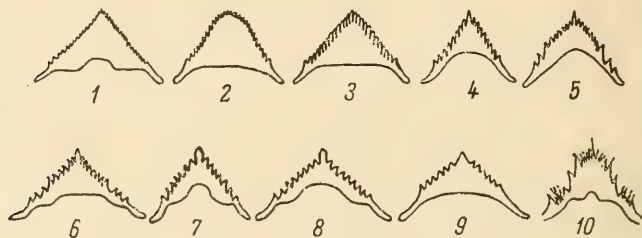
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Fig. 43. Structure of labium in the 4th instar larvae.

ge—gena; gus—gular suture; md—mandible; mnt—mentum; prmt—prementum; smt—submentum.

forming articular processes by which the prementum is freely articulated with the gular suture (Fig. 41, *gus*). Furthermore, the prementum is joined to the mandibles (Fig. 43, *md*) and to the hypopharynx. Pointed-ended teeth turned apically are situated along the margins of the triangular prementum. The nature and number of these teeth vary greatly (Fig. 44); therefore, attempts to use this feature in the systematic classification of mosquitoes (Dyar, 1922; Felt, 1904; Howard, Dyar and Knab, 1913, 1915; Theobald, 1901–10) have been unsuccessful. We note that in the members of the subgenus *Culiseta* s. str. the teeth are numerous, but small and the apical teeth are not prominent. However, in larvae of *Culicella* (Fig. 44, 5–7), the teeth are fewer and stronger and the apical tooth stands out prominently at least among the adjoining teeth due to its size.

The hypopharynx represents a complex formation in the form of a heavily sclerotized plate with strong teeth. It is situated posterior to the prementum forming a dome-like uprising of the oral cavity. Cook's (1949) study of this organ in *Culiseta incidens* reveals a very complex structure (Fig. 45). One of the main functions of the mentum is to pass the food bolus into the pharynx. The bolus is partly



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Fig. 44. Types (1–10) of structure of prementum in different *Culisetina*.



Fig. 45. Structure of hypopharynx in the 4th instar larva of *Culiseta incidens* (after Cook, 1949).

d—dorsal view; *v*—ventral surface.

broken by the striking of the maxillary teeth on the large teeth of the mentum as on an anvil. Closely associated with the sclerotized pharyngeal rings and valves, the hypopharynx additionally controls to some extent the pharyngeal tube and the swallowing of the food.

In sum, the 4th instar larvae of all members of Culisetina studied can be placed in 3 groups and 5 classes according to the structure and function of the oral organs (Table 3).

65 The larva of *Allotheobaldia longiareolata* has a special position and can tentatively be placed in the first group of periphytophages, with some liberal interpretation.

The larvae of the younger stages, while preserving the essential features of the mouth parts typical of the species, differ in their relatively greater primitiveness. The mouth parts, especially in larvae of the 1st and 2nd instars can be considered an intermediary type with a predominant tendency to filter feeding.

Thorax: In the larvae of Culisetina, as in all other mosquitoes, the thoracic segments are completely fused. The width of the thorax noticeably exceeds that of the head in the subgenus *Culiseta* s. str. in which the mean values of the head-thorax index (percentage ratio of the maximum width of head to the maximum width of thorax) vary in the different species between 65.4 and 81.3%. Similar data have been found for *A. longiareolata* (70.8%). As a result of significant cephalic enlargement, the head-thorax index is about one (95.6–99.0%) in filter feeders of the subgenera *Culicella* and *Climacura*.

Setae are found on the thorax in three groups corresponding to the pro-, meso- and metathorax. Each group consists of 14 pairs of

setae of different sizes. Some are set on the highly convex dorsal surface (1-6) and others on the thoracic callosities; one seta (13) occupies the ventral position. In the larvae of Culisetina, the dorsal setae, with the exception of the prothoracic, are usually poorly developed as are the ventral ones. On the prothorax of all Culisetina, the dorsal setae are located on the anterior margin (Figs. 46 and 47). The first three are set close to each other and their sclerotized bases are fused into a single complex. In *Culiseta* s. str. and *A. longiareolata*, these, like the other dorsal setae of the prothorax, are small with a varying number of branches, especially the setae 3, 4 and 5 (Fig. 46). In *Culicella*, the dorsal setae of the prothorax have a small number of branches, but with significantly greater dimensions and thickness (Fig. 47). Their length, especially that of seta 3, could exceed the length of the thorax and hence the ends of these setae (3-6) turned anteriorly are seen along the anterior margin of the head. Dorsal setae of the meso- and metathorax, as a rule, are even weaker than those of the prothorax. In the subgenus *Culicella*, they are hardly noticeable; in other cases, the first three are rudimentary and setae 4-6 are visible (Fig. 47). The lateral setae on all thoracic segments (Figs. 46 and 47) are well developed. In *Culicella* (Fig. 47) and *Climacura*, they are very long and single branched in most cases (Fig. 46) while, in the other larvae, they are shorter with pubescence and a greater degree of branching, especially setae 8-10 on all segments of *A. longiareolata*. Setae 9-12, representing the complex of pleural setae, are set on a common, heavily sclerotized base. In the subgenus

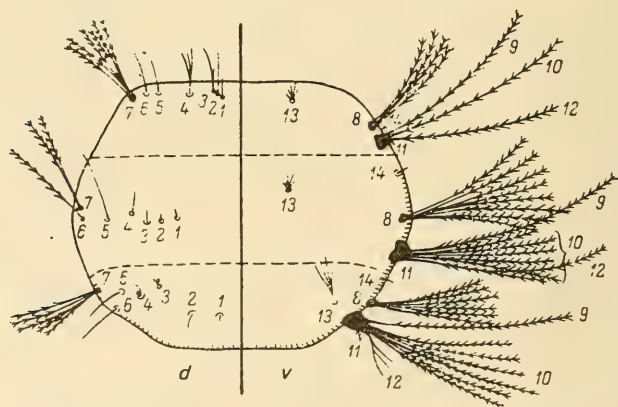


Fig. 46. Chaetotaxy of thorax in the 4th instar larvae of the subgenus *Culiseta* s. str. (*C. bergrothi*).

d—dorsal setae; v—ventral setae; numerals denote their numbers.

Culiseta s. str., the prothoracic pleural setae 9, 10 and 12 are long, simple and pubescent (Fig. 46); on the mesothorax, the long setae 9 and 12 are usually single and unbranched, while 10 is the palmate type (Fig. 46); on the metathorax, seta 12 is greatly weakened, 9 single, unbranched and 10 palmate (Fig. 46). Seta 11 in all *Culiseta* is rudimentary as is seta 13 and usually 14.

All thoracic setae in *Culicella* larvae, unlike those in *Culiseta* s. str. and *A. longiareolata*, are smooth or have pubescence. Edwards (1930) noted the presence of especially small dendritic setae located dorsolaterally on the thorax and abdomen of *Theomyia fraseri*.

Occasional attempts have been made to use the thoracic chaetotaxy in the systematics of mosquito larvae. Our data indicate that differences among the individual groups of *Culisetina*, their subgenera and genera, are perceptible. However, this is not so for species-wise differences, since thoracic chaetotaxy varies widely in each species and at the same time the variation is uniform in different species of the same subgenus (Siribaed, 1936). In other genera of the family Culicidae, which are very far apart, the nature of thoracic chaetotaxy may be similar to either *Culiseta* s. str. (in larvae with mixed feeding and periphytophages) or *Culicella* (in larvae of filter feeders). Similarity in thoracic chaetotaxy not only in the various species of the same subgenus, but in various genera often far removed from each other and, at the same time, critical differences in

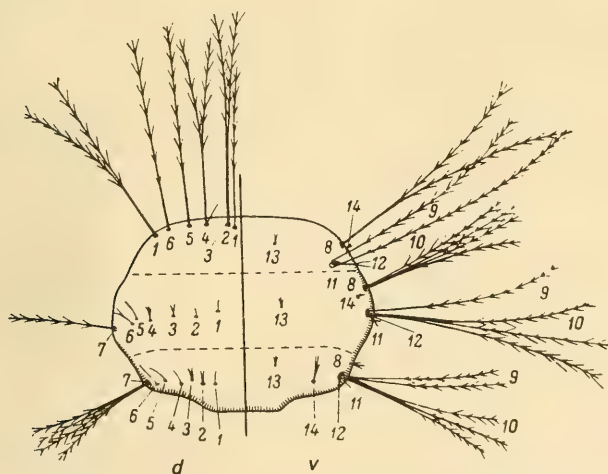


Fig. 47. Thoracic chaetotaxy in the 4th instar larvae of the subgenus *Culicella* (*C. morsitans morsitans*).
(Legends same as in Fig. 46)

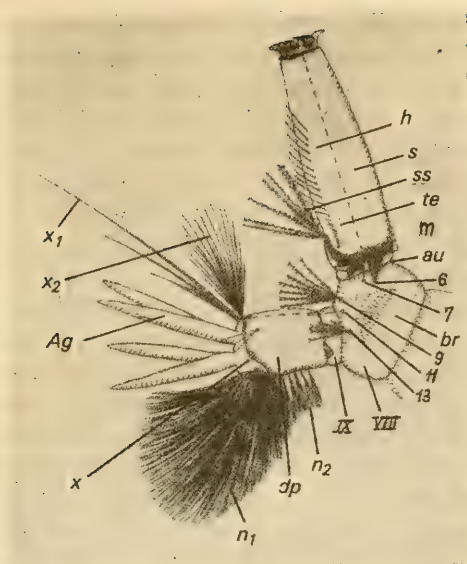
the various subgenera within a given genus can be explained by the normal, uniform functional variations adapted to the type of feeding (surface feeding, filter-feeding, mixed, periphyton and predatory).

- 67 A pair of large thin-walled air sacs (with hydrostatic function) are well developed in the thorax of the larvae of the African *Theomyia fraseri*. They are found among Culicinae only in Toxorhynchitini, *Mansonia* and *Orthopodomyia* (Edwards, 1932a). In other Culisetina, such air sacs are absent and only slightly enlarged trachea are present.

In the thoracic development of the 1st to 4th instar larvae, apart from increases in size, we found growth of the setae and their branches, which in the first stage larvae are usually all simple. The *Culicella* larvae are an exception. In these forms from the 1st to the 3rd stages, there is an increase in the number of branches of some setae (7-14-prothoracic, 8-10-mesothoracic, 7-11-metathoracic) while later, in the 4th instar larvae, these setae are less branched than in the 3rd instar larvae.

Abdomen: As in other members of family Culicidae, the abdomen of Culisetina larvae consists of 9 distinctly isolated segments. However, a detailed study of the segmental composition of the abdomen (Martini, 1929-31; Monchadskii, 1936, 1937, 1951) enabled us, to establish that the abdomen originally consisted of 10 segments as still preserved in Dixidae. In all other mosquito larvae, however, because of the development of a specialized respiratory apparatus, the primary eighth and ninth segments fused into a single one with the formation of a secondary eighth segment, which may be called the respiratory segment. The tenth segment thus became the secondary ninth segment. This should be called the anal segment to avoid confusion since the remnants of the true ninth segment are preserved in Culisetina, as in many other Culicidae, in the form of a fairly narrow ring between the respiratory and anal segments (Fig. 48, IX).

The first 7 abdominal segments are the same type, each in the form of a flattened ring. Furthermore, the anterior ring is larger in diameter, gradually tapering posteriorly so that the abdomen as a whole, in its first 7 segments, has a cylindrical form tapering posteriorly. On each of the 7 segments there is a set of 13-14 pairs of setae designated serially. They are situated symmetrically, close to the posterior margin of the segment, and form two irregular, zig-zag semicircles from the dorsal to the ventral sides. In all Culisetina, the nature of these abdominal setae is similar on all 7 segments. In the larvae of *Culiseta* s. str. and *Allotheobaldia longiareolata*, setae 4-10



68 Fig. 48. Structure of the posterior end of the body of the 4th instar larvae. Roman numerals denote segments and Arabic numerals the setae of posterior brushes.

ag—anal gills; br—brush [comb]; s—siphon; ss—siphon setae; te [pecten] teeth; h—seta on siphon crest; au—auriculate process of siphon sclerotization; dp—dorsal plate [saddle]; n_1 and n_2 —ventral brush to it; x_1 and x_2 —outer and inner dorsal seta. Broken lines on the siphon and saddle denote the lines of measurement of the length of these organs.

are most developed, relatively short and branched, compared to the corresponding setae in *Culicella* and *Climacura*.

The respiratory segment (Fig. 48, VIII) carries the respiratory siphon and, as a result, its form is altered. In the proximal portion, it is ring-shaped and later its surface is sharply cut angularly on the dorsal and ventral posterior halves. On the dorsal sharp edge rests the siphon base turned posteriorly and upward while a narrow ring (remnant of the ninth segment) is attached to the ventral sharp edge. The last anal segment turned posteriorly and downward is attached to the narrow ring above. Numerous scales [comb scales] are set on the sides of the respiratory segment. Together these scales form, on each side, the brushes [combs] (Fig. 48, br), usually in the form of triangular or trapezoidal spots with the apex turned posteriorly. Each scale of the comb (Figs. 51 and 54) bears an elongated base set in a suitable cuticular pit and projecting body carrying the setae,

teeth and spines in different numbers and of different dimensions. The form of the spines and the nature of their crenation are visually specific and, in spite of their variability, can be used as a systematic feature. Thus, in *C. bergrothi*, the typical scales carry a long narrow body sometimes slightly pinched close to the base and a rounded
 68 apex with comparatively long spinules, which are sparser and smaller toward the base. In *C. glaphyoptera*, the scales have a broad base and a broad apex so that the median narrowing of scales is distinct. The apex is rounded in the long, densely set spinules, which may be absent in the narrow zone in the middle. Typical of *C. alaskaensis* is the absence of median thinning of the scales. The scales are the shortest in *C. niveitaeniata*; in *C. silvestris ochroptera*, there is a darkly pigmented longitudinal band on the body of the scales at least in the distal (according to Peus, 1935) comb. We find a similar pattern in *C. silvestris amurensis* in which, as demonstrated by Monchadskii (1947, 1951) scale variation is greatest. The variation of scale form has been noticed not only in the different specimens of the same species but in the different scales in the comb of the same larva. Usually, the extreme scales differ greatly from those at the center of the comb; the latter are considered typical. The number of scales in a comb invariably increases from stage to stage and the variation is numerically significant. Interestingly, in a given specimen, the combs on the right and left often bear a significantly different number of scales and the difference between the lowest and highest numbers could be 20-30% or more (up to 38% in *C. bergrothi*). Monchadskii (1951, p. 126) noted an even greater difference in the case of *C. alaskaensis*: from 36 to 52 scales, that is, 44%. Nevertheless, there is a specific pattern of increase in the number of scales in relation to the nature of feeding. While the average number of scales in the comb does not exceed 50 in typical periphytophages (*Allothobaldia longiareolata*, *Culiseta annulata*, and others), not only the average number of scales but their minimal number exceeds 50 in larvae with mixed feeding (*Culiseta bergrothi*, *C. glaphyoptera* and *C. niveitaeniata*), and their average number is over 100 in the specific filter feeders *Culicella*. The larvae of *Culicella silvestris amurensis* in which there are only 78.1 ± 0.33 (60-100) scales in the comb constitute an exception*. The functional importance of this feature is not yet clearly understood.

Only 5 of the complete set of 13-14 pairs of setae are preserved on

*A.S. Monchadskii (1936, 1951) noted an average of 50 comb scales for *C. fumipennis* while they are not less than 100 according to Marshall (1938).

the respiratory segment itself (rarely more). They surround the comb along the posterior margin of the segment. They are variously designated by different investigators. Sometimes they are marked serially from 1 to 5, top to bottom; others use the initial letters of the Greek alphabet (Marshall, 1938). Martini (1929-31) numbered the setae of the larvae of *Anopheles* corresponding to the analogous seta of the normal ventral segment. This system is now used even in larvae of Culicinae (Monchadskii, 1936, 1951). We follow this numeration too (Fig. 48). The extreme upper (6), median (9) and extreme lower (13), especially the median, are pubescent and well developed compared to the smooth intermediary ones (7 and 11). This feature is often used in the systematics of mosquito larvae. However, for Culisetina, it cannot be extensively applied since, with a few exceptions, branching of these setae is significant and highly variable. In the members of the subgenus *Culicella*, all of them are somewhat longer and less branched than in the subgenus *Culiseta* s. str. In *Allotheobaldia longiareolata*, the extreme [upper and lower] setae are less branched, while the median (9), on the contrary, have maximum branching compared to all other larvae which have been studied.

The most important new structure in Culicinae larvae, the respiratory siphon, is in the form of a fairly heavily sclerotized projection of the dorsal wall of the secondary eighth (respiratory) segment with the stigmatic apparatus at its apex. The sclerotization of the siphon in the 1st stage larvae of all Culisetina does not cover the entire siphon, but only the apical one-third or one-half (Fig. 49). Furthermore, the boundaries of the primary and secondary sclerotization are easily distinguishable (Fig. 49) even in other Culicinae. During metamorphosis, sclerotization increases although the pattern characteristic of the younger larva is often preserved even in the 2nd

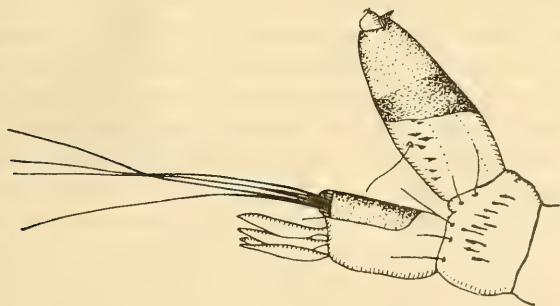


Fig. 49. Posterior end of the 1st instar larva of *Culiseta bergrothi*.

instar larva (Maslov, 1963). Sometimes, this is achieved only in the 3rd or 4th stage but, in *A. longiareolata*, the sclerotized portion of the siphon does not reach its base even in the 4th stage larvae (Fig. 98, *d*). The base itself of the sclerotized portion of the siphon is usually flattened in the form of an incomplete ring, sometimes thickened, gradually weakening ventrally, where a fairly deep groove is formed. It is particularly deep in *A. longiareolata* larvae in which the basal rings are actually absent in the siphon. Two processes, the auricles, are formed along the basal sides of the siphon tube (Fig. 48, *s*) and firmly hold the transverse musculature of the siphon; the auricles permit the siphon to extend slightly posteriorly. This function is important in the emergence of the larva from the water surface (Maslov, 1964b). The ventral groove found in the sclerotized portion of the base facilitates this movement. The auricles are present in the 4th stage larvae of all *Culiseta*, but are absent in *A. longiareolata* (Fig. 98, *d*), *Theomyia fraseri* (Fig. 97, *b*) and *Austrotheobaldia littleri* (Fig. 96, *b*). In the younger larval stages of *Culiseta*, their presence depends on the degree of development of the sclerotized portion of the siphon tube.

- Siphon length in the larvae of Culicinae varies as does its form.
- 70 In Culisetina, the siphon is invariably distinctly narrow apically. The siphon index, that is, the ratio of the length of the siphon to the width (diameter) of its base, has long been used to describe the relative length of the siphon, one of the vital systematic features of Culicinae larvae. Therefore, this index is called either simply siphon index or the first siphon index (I) to distinguish it from the second siphon index (II) (see below). As Monchadskii (1936, 1951) demonstrated, very different siphon index values are obtained depending on the method of measurement. To avoid confusion, a study of these characteristics has been conducted according to the rules proposed by Monchadskii (1936, p. 44): (1) the siphon is measured laterally, (2) the length of the siphon is measured without the stigmatic plate valves from the base of the auricular processes of the basal ring of the siphon to the posterior margin of the distal end at the base of the posterior pair of valves; (3) the width of the siphon base is measured along the line running from the anterior margin of the siphon base, through the base of the auricular processes to the point of its intersection with the posterior margin of the siphon base and sometimes with the continuation of this margin, if there is an incision at the base of the rear side (Fig. 48).

When the auricles are absent, the siphon length is measured along the lateral line from the anterior corner of the base to the apex

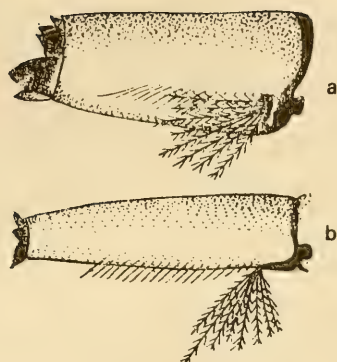


Fig. 50. Short (a) and long (b) siphons in the 4th instar larva of *Culiseta bergrothi*.

near the anterior valve of the stigmatic plate (Fig. 98, d). While measuring, care must be taken to avoid crushing the siphon in the specimen. Otherwise, the results obtained will be unreliable and invalid. To calculate the siphon indices given below we have used the results of measurements using fresh or preserved specimens or even samples with a wax base.

Generally, in all Culicinae, the larvae of filter feeders have a very long* and thin siphon with an index rarely less than 5 while the primary siphon index in the larvae of periphytophages is usually much less than 4, decreasing in some cases (*Allotheobaldia longiareolata*) to 1.5 or less. Marshall's report (1938, Table XI, p. 105) that the siphon index for *Culiseta fumipennis* varies from 3.8 to 4.8 is clearly an underestimation. In the figures in his own work (Fig. 61, p. 90 and Fig. 137, p. 224), the relative length of the siphon in *C. fumipennis* differs little from that of *C. morsitans* (Fig. 138, p. 228) and is close to 5; the works of Rioux (1958) and Senevet and Andarelli (1959a) present similar data. In all Culisetina, the variation range of the primary siphon index of larvae is much greater (Maslov, 1952, 1963 and others). The illustrations given (Fig. 50) confirm this variation in the example of *C. bergrothi* in which the range between the extreme values of the primary siphon index (2.4–4.8) attains, as in *C. alaskaensis*, a record figure of 100%. Such a wide variation is

*The larvae have a long siphon capable of holding a large volume of water without withdrawing from the substratum (or the water surface); herein lies the advantage of the long siphon in the filter feeders (Maslov, 1952, 1961a, 1963 and Monchadskii, 1937).

undoubtedly due to the diversity of habitat and growth of the larvae as demonstrated for the larvae of *C. bergrothi* growing under different conditions of feeding (Maslov, 1952, 1961a, 1963; and others).

- 71 Other siphon indices, apart from the ratio of siphon length to its basal width, are also used. To describe the siphon form (extent of its apical narrowing), Monchadskii proposed, especially for *Culiseta*, the ratio of siphon length to apical width or the ratio of basal width to its apical width or a comparative ratio of siphon length to its basal and apical widths (1936, p. 44). One of these values, the ratio of basal to apical width of the siphon, will therefore be called the second siphon index (II). However, unlike the suggestion of Monchadskii (1951), these indices should not be regarded as unimportant systematic features. A comparison of the author's numerical data (Maslov, 1963) for *C. alaskaensis* and *C. annulata annulata* with the corresponding data of Monchadskii (1951, pp. 127-131) reveals some discrepancies. For *C. alaskaensis*, Monchadskii gave a second siphon index of 1.2-1.4 (average 1.3) and for *C. annulata annulata* 1.6. A study of *C. alaskaensis alaskaensis* and *C. alaskaensis indica* from different regions somewhat broadened the variation range of the second siphon index from 1.2-1.6 in the former subspecies and from 1.3-1.8 in the latter. The average values are particularly close: 1.32 ± 0.004 and 1.42 ± 0.006 ($n_1=409$ and $n_2=217$). The second siphon index of *C. annulata* is also variable within roughly the same limits except that the average value of the index in *C. annulata annulata* is actually somewhat higher (1.62 ± 0.013). The uniform variation of this feature is found not only in the different species of the subgenus *Culiseta* s. str. but also when compared with species of the subgenus *Culicella*. The larvae of *Allotheobaldia longiareolata* are an exception; here the mean value of the second siphon index is noticeably higher than in the others (1.76 ± 0.009) and the range of variation (1.3-2.3) is still wider.

Nevertheless, attempts to provide a numerical definition to the siphon form resulted in yet another index (Ks) which, in the author's view, better reflects the extent of siphon pinching. This coefficient of siphon tapering (Ks) represents the difference between the basal (Sho) and apical (Shv) widths of the siphon in relation to its length (D); expressed as a percentage, it is $Ks = \frac{(Sho-Shv)}{D} \times 100\%$.

While the differences in the coefficient of siphon narrowing between the species and subspecies of a given subgenus are not very striking, the differences between the subgenera are fully perceptible. Among the members of the subgenus *Culiseta* s. str., the mean value of the

coefficient K_s in most cases exceeds 10% and does not reach 20% while in *Culicella* the average value of K_s is not more than 7% and the maximum is 10%. The larvae of *A. longiareolata* differ distinctly from all others; in this respect, the coefficient K_s varies from 12 to 36%; the average is 25.7%. The ratio of the length of the siphon to that of the head is interesting, if not in terms of systematics, at least ecologically. In the larvae of the subgenus *Culiseta* s. str. this ratio averages 1.5–1.6. In *A. longiareolata*, it is even less 0.8 to 1.3; $\text{mean} = 1.03 \pm 0.004$. In the subgenus *Culicella*, on the contrary, it is high, 2.0 or more.

Apart from the siphon indices discussed above, various other indices have been used by different scientists. Colless (1957) suggested defining siphon form by the ratio of its length (L) to the length of the saddle (S); Senevet and Andarelli (1959b) used Colless' index (L : S) and derived one more: the ratio of siphon width (1) to the length of the saddle, 1:S.

The siphon dimensions are related to the method of feeding. In the larvae of filter feeders, the siphon is longer and its ratio to the length of the head is greater than in periphytophages. In the euri-
72 tropic larvae of *Culiseta bergrothi*, the relative length of the siphon and correspondingly its ratio to the length of the head under filter-feeding conditions are similarly high although not invariably (Maslov, 1952, 1961a and 1963).

Culisetina larvae have only one pair of siphon setae at the base of the siphon, except members of the subgenus *Climacura* (Figs. 85, c; 86, c and 88, b) and Australian *Austrotheobaldia littleri* (Fig. 96, b). However, basal placement of siphon setae is known even in the larvae of Toxorhynchitini, Indo-African *Hodgesia* and some other tropical mosquitoes. The siphon setae may be set at the base or near the basal margin of the sclerotized tube (*Allotheobaldia longiareolata* Fig. 98, d, *Culiseta morsitans*, Fig. 78, c and *C. silvestris amurensis*, Fig. 81, b), but more often they are further away, on the tube near the siphon crest* and invariably below it. The larvae of the subgenus *Climacura* are of course, an exception (Figs. 85, c, d; 86, c and 88, b): here a pair of small, palmate setae are found basally between the teeth of the crest; additionally, there are short palmate setae forming a median-ventral row from the crest to the apex of the siphon and a few pairs of small setae are found on the siphon dorso-laterally or ventro-laterally (Belkin, 1962; Carpenter and La

*The term siphon crest refers to both the pecten and the row of single setae distal to the pecten as in *Culiseta inornata*, Fig. 70, c [editor].

Casse, 1955; Dobrotworsky, 1962 and Matheson, 1929, 1944). On the dorsal surface of the siphon even in other *Culisetina* there are a pair of single or paired, small setae. The siphon seta consists of a few usually fairly dense pubescent branches either in the shape of fan branches arranged in a single plane (Fig. 31), as in *A. longiareolata*, or along the pyramidal ribs in most *Culiseta* (Fig. 31). There are also many cases in which the effective branching of the siphon seta bears an intermediary, cone-like structure as in *C. bergrothi* and more rarely in the other members of *Culiseta* s. str. Moreover, in the preserved specimens we found a false, apparently fan-like arrangement of conical setae when all their branches are distributed in a single plane under the pressure of the cover slip. In such cases, careful study of the setal bases using a high power ($40\times$) microscope will reveal the actual nature of the branching.

The number of branches in the siphon seta is variable. Generally there is a high level of branching in the larvae of periphytophages of the subgenus *Culiseta* s. str. and *Allotheobaldia longiareolata*. The maximum number of branches has been recorded in *A. longiareolata*, an average of 11.7 ± 0.037 with a range of 8–15. Barraud (1924) gave an even higher figure of 15–20 branches for the Indian members of this species. In the African *Theomyia fraseri* (Edwards, 1930) and in the Australian *Austrotheobaldia littleri* (Dobrotworsky, 1954), the siphon seta is simple (Figs. 97, *b* and 96, *b*). Other Australian members belonging to the subgenera *Neotheobaldia* and *Culicella* also have one, usually two-branched siphon setae, which in any case are poorly developed (Dobrotworsky, 1954; Lee, 1937, 1944) (Fig. 77). In younger stage larvae, there is less branching of the siphon setae and they are invariably simple in 1st stage larvae (Table 4).

Also variable is the relative length of the seta, usually expressed in the form of a siphon seta index, that is, the ratio of the length of the longest branch of the seta to the length of the siphon. In some cases, this index is used as a systematic feature, for example, in differentiating such species as *Culiseta fumipennis* with an index of over 0.5 and *C. morsitans* with an index of 0.4 ± 0.005 (range 0.28–0.58). Monchadskii (1951) gave an even lower value of 0.24–0.28 for *C. morsitans*.

- 73 The crest (Fig. 48, *te* and *h*), in the form of two rows of teeth, spines and setae, covers the basal portion of the siphon, to some extent even extending toward the apex. Often, some teeth of the crest project forward beyond the sclerotized tube. These teeth (Figs. 31 and 51) may be simple, flexed or straight. In other instances, they have crenations in the form of isolated or more numerous basal

denticles, denser as a rule toward the apex of the tooth. With the growth of additional crenations, the tooth base becomes increasingly broad. With further development of crenation, the pecten tooth acquires a flabellate form (Fig. 51). In some cases, the teeth of the crest are distinctly paired (*Theomyia fraseri*, Fig. 97, b). Usually, the teeth gradually become weaker proximally and the extreme proximal ones appear rudimentary. The form of the pecten teeth is variable not only in different species and different specimens of the same species, but in different teeth of the same crest.



Fig. 51. Types of setae (1-8), teeth and spines of siphon crest (9-17) and comb scales (18-27) in the 4th instar larvae.

1—microtrichia; 2—short seta; 3—long and straight seta; 4—long and thin seta; 5—long and flexed; 6—long with bent portion; 7—thick and hook-shaped seta; 8—thick and obtuse seta; 9—hair-like tooth; 10—normal tooth in the crest of *Culiseta* s. str.; 11—broad tooth; 12—short and spine-like tooth; 13—paired tooth of the crest (only in *Theomyia fraseri*); 14 and 15—rudimentary tooth; 16 and 17—short and long spine; 18—short, symmetrically soft and pubescent; 19—short, asymmetrically soft and pubescent comb scale; 20—short, symmetrically rigid and crenated comb scale; 21—short, asymmetrically flexible and crenated comb scale; 22—long, pointed and spiny comb scale; 23—the same; 24—long, symmetrical, soft and pubescent comb scale; 25—long, asymmetrical flexible and pubescent; 26—long and asymmetrical crenated; 27—long comb scale with narrow middle region.

Table 4. Stadium-wise difference in the larvae of *Culiseta bergrothi* Edw. based on the important morphological features

Characteristic	First instar (n = 95)		Second instar (n = 117)		Third instar (n = 134)		Fourth instar (n = 1,592-3,031)	
	Range	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range	Mean $\pm$ SE
1. Length of head (mm)	0.25-0.35	0.29 $\pm$ 0.003	0.40-0.65	0.50 $\pm$ 0.005	0.7-0.9	0.79 $\pm$ 0.04	0.8-1.6	1.12 $\pm$ 0.01
2. Color of head (class)	5-8	6.1 $\pm$ 0.08	4-7	5.2 $\pm$ 0.07	4-7	4.9 $\pm$ 0.08	1-8	4.4 $\pm$ 0.03
3. Egg tooth	Present		Absent		Absent		Absent	
4. Compound eyes	Absent		Absent		Poorly developed		Present	
5. Head index	1.0-1.3	1.12 $\pm$ 0.004	1.1-1.4	1.31 $\pm$ 0.004	1.2-1.5	1.38 $\pm$ 0.003	1.2-1.17	1.46 $\pm$ 0.002
6. Number of setae in the antennal tuft	1-3	1.9 $\pm$ 0.07	4-9	5.7 $\pm$ 0.09	4-9	6.0 $\pm$ 0.09	5-19	12.4 $\pm$ 0.06
7. Branching of outer frontal seta	1	1	4-7	4.8 $\pm$ 0.07	5-10	6.5 $\pm$ 0.09	8-18	10.4 $\pm$ 0.06
8. Branching of median frontal seta	1	1	2-4	2.4 $\pm$ 0.05	2-5	3.1 $\pm$ 0.05	4-14	9.2 $\pm$ 0.04
9. Branching of inner frontal seta	1	1	2-5	3.1 $\pm$ 0.06	4-9	5.5 $\pm$ 0.09	5-13	9.5 $\pm$ 0.03
10. Siphon length (mm)	0.2-0.3	0.26 $\pm$ 0.004	0.5-0.7	0.61 $\pm$ 0.007	0.8-1.0	0.96 $\pm$ 0.006	1.2-2.1	1.54 $\pm$ 0.01
11. Separation of primary and secondary sclerotization of siphon	Distinct		Absent		Absent		Absent	
12. Branching of siphon seta	1	1	2-5	3.4 $\pm$ 0.08	3-6	4.6 $\pm$ 0.09	4-10	7.1 $\pm$ 0.02
13. Number of teeth on crest	3-8	6.1 $\pm$ 0.08	6-10	7.7 $\pm$ 0.07	6-14	12.0 $\pm$ 0.11	11-23	19.4 $\pm$ 0.02
14. Number of setae on crest	Absent		2-3	2.1	4-8	5.8	6-18	11.9 $\pm$ 0.04
15. Nature of saddle	Incomplete		Incomplete		Incomplete		Complete	
16. Number of ventral brush setae on the common base	Absent		6-12	9.1 $\pm$ 0.10	9-14	11.0 $\pm$ 0.08	13-19	16.1 $\pm$ 0.02
17. Number of ventral brush setae anterior of common base	Absent		6-10	8.2 $\pm$ 0.08	5-9	7.0 $\pm$ 0.07	3-5	3.1 $\pm$ 0.01
18. Gill index	0.6-1.5	1.01 $\pm$ 0.02	0.6-2.0	1.11 $\pm$ 0.03	0.5-2.6	1.46 $\pm$ 0.03	0.8-3.0	1.84 $\pm$ 0.03

In the larvae of the subgenus *Culiseta* s. str. only the proximal half of the crest is formed by the teeth. Farther away from the base, the teeth are elongated, while the additional crenation weakens and the tooth is gradually transformed, initially into a flexed long tooth with a small basal crenation and later into a seta (Fig. 32). Thus, in the larvae of the subgenus *Culiseta* s. str., each crest consists of a row of teeth at the base extending farther toward the apex in the form of a seta (Fig. 48). The crest then may be in the form of a straight or slightly bent row of teeth and setae set at equal distances from each other. In other cases, even among the different members of a given
 74 species, the regularity of the row of teeth is often disrupted: the distances between them vary, individual teeth are displaced from the row either dorsally or ventrally and so on. The crests of the 4th-instar larvae of *Allotheobaldia longiareolata* and *Culiseta fumipennis* are particularly irregular.

The number of teeth and setae (when present) on the crest vary widely. Especially in the larvae of *C. bergrothi*, the average number of teeth is 19.4 ± 0.016 (range 11–29) and setae 13.8 ± 0.036 (range 8–18); in *C. annulata subochrea*, the number of teeth is 14.8 ± 0.110 (9–12) and setae 19.3 ± 0.149 (11–27). Monchadskii (1936, 1951) gave an even broader range of variations for these and some other species. Furthermore, while describing the individual species of larvae, Monchadskii separately records the crest teeth as normal and rudimentary (1951, pp. 125, 127, 132, 134, and others) which is hardly justifiable, since it is very often difficult to demarcate where the normal teeth end and the rudimentary ones begin.

The stigmatic plate at the apex of the siphon has been well described by Monchadskii (1930, 1936, 1947, 1951) for many larvae of Culicidae. Its design is shown in Fig. 52 (after Monchadskii). The author has not conducted any special investigations nor does he have any reference material concerning this feature in most members of Culisetina; a precise description of the structure of this organ in Culisetina larvae is not available although the structure is probably of systematic significance and exceptional functional importance. With the example of *Culiseta alaskaensis* (subgenus *Culiseta* s. str.), *C. morsitans* (subgenus *Culicella*) and *Allotheobaldia longiareolata*, Monchadskii (1930) analyzed the characteristics of the stigmatic apparatus and its development from the first to the last larval instar stage for the three main groups of the subtribe Culisetina.

The last anal segment of the abdomen is relatively short in some cases (subgenus *Culiseta* s. str.), the ratio of its length to diameter does not exceed or only slightly exceeds one (Fig. 48). In other cases

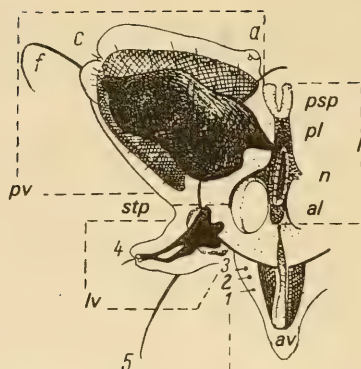


Fig. 52. Structure of stigmatic plate (surface view) (after Monchadskii, 1930).

pv, *lv* and *av*—posterior, lateral and anterior valves; *l*—lever; *al* and *pl*—anterior and posterior arms of lever; *psp*—posterior process; *stp*—stigmatic process; *n*—lever arm (*a*, *c* and *f*) and 1–5—numbers of setae.

(subgenus *Culicella*), the anal segment is longer and the ratio of its length to diameter is about 1.6. The integument of the anal segment has a heavily sclerotized section—saddle—which in all larvae of younger stages (1st–3rd) covers only the dorsal portion of the anal segment in the form of a ring. The 4th-instar larvae of *A. longiareolata* with only the dorsal peak are an exception (Fig. 98, *d*).

There is a weak seta on the surface of the saddle in the median line or close to its posterior margin. Apart from this seta, there are two pairs of caudal setae posterior to the saddle on the dorsal surface of the anal segment (Fig. 48). Of these, the outer ones are much longer, thicker and less branched than the inner ones, often seen as an intensely developed flabellum consisting of 15–20 or more branches. Both the outer and inner caudal setae are simple only in *Theomyia fraseri* (Fig. 97, *b*).

- 75 The ventral portion of the anal segment has one of the most important organs of movement, the ventral brush (Fig. 48, *n*₁ and *n*₂). This is absent only in the first instar larva (Fig. 49). The ventral brush consists of a group of flexed and specially branched setae of different lengths. The branching of each seta in *Culisetina* larvae occurs in the same plane, longitudinally, on both sides of a short main shaft (Fig. 31). Together the ventral brush forms an asymmetrical flabellum set perpendicular to the frontal body plane and set downwards and posteriorly (Fig. 48). Furthermore, the setae are not

set in a straight line, but their "roots" alternate in a zigzag fashion to the right and left of the midline of the ventral brush base. The shaft of each seta has basal lateral processes of different lengths; if the seta takes the position to the left on the zigzag row, the processes on its right are more strongly developed and vice versa. The ends of all these processes are joined together to form a firm, strongly sclerotized frame called the general base of the fin* [transverse grid bar]. Anteriorly, the ventral brush setae gradually becomes shorter and less branched (Fig. 48). Some of the anteriormost ones, the shortest and least branched setae, are set not on the transverse grid bar, but anterior to it. Some of them pierce the ventral portion of the saddle at the base. Exceptions are the larvae of the African *Theomyia fraseri*, Australian *Neotheobaldia* and *Austrotheobaldia littleri*, in which all the ventral brush setae are set on the general base (Figs. 89, c; 91, c; 96, b and 97, b). The ventral brush structure is often of significance in the systematics of mosquito larvae including *Culisetina* (Marshall, 1938; Martini, 1928-1931; Monchadskii, 1936, 1951; Natvig, 1948). However, in each subgenus, the number of setae on the common base and the number anterior to the common base vary so widely in each species and the variation is so uniform in the different species that this feature can also be used in systematics. The same is true of the number of setae piercing the ventral portion of the saddle and of the number of branches in each seta. At the same time, there is a specific difference between the larvae of filter feeders (*Culicella*) and of scrapers (*Culiseta* s. str. and *Allotheobaldia longiareolata*). In the former (filter feeders), there is a smaller number of prominent setae set on the common base and all of them are comparatively less developed, but there are more setae anterior to the common base (Figs. 78, c; 81, b) than in periphytophagous scrapers (Figs. 59, c; 61, c).

In immature larvae (except the first instar in which the gills are absent) compared with those of the 4th stage, there is a great reduction in the number of ventral brush setae set on the common base but simultaneously the number of setae anterior to the common base increases (Table 4). A systematic stagewise intensification of the basal portion of the ventral brush is very typical of scraper larvae.

Two pairs of anal gills are found at the extreme end of the last segment surrounding the anal pore into which they can be slightly drawn with the typical musculature. The gills are in the form of

*Old nomenclature: folded portion according to Shtakel'berg 1937; Fachertrager according to Martini (1929, 1931).

transparent, colorless, thin walled outgrowths of integument devoid of epicuticle and enriched with chitin as a result of which they are highly impervious to water (Kuznetsov, 1951; Semenova, 1959; Shvanvich, 1949; Wigglesworth, 1954). In most Culisetina, the upper and lower gills are identical in dimensions. Only *Allotheobaldia longiareolata* and *Theomyia fraseri* are exceptions: in these, the upper gills are longer than the lower ones (Figs. 97, *b* and 98, *d*) while the upper gills are slightly shorter than the lower ones in *Culiseta kanayamensis* (La Casse and Yamaguti, 1950). We know that the relative length of anal gills—the gill index*—is highly variable; therefore the use of this factor for practical systematics has serious limitations (Maslov, 1962b, 1963). The functions of anal gills are numerous. They perform the respiratory functions primarily by exhaling carbon dioxide (Wigglesworth, 1933a, 1933b; Almazova cited by Beklemishev, 1944) and to a lesser extent through oxygen intake. But the respiratory functions are not the basic function of anal gills. Apart from the special stigmatic apparatus, this function is performed by the entire body surface. Intestinal breathing is also vitally important. Excretion and osmoregulation are the more vital and basic functions of the anal gills (Kuznetsov, 1948; Martini, 1922; Maslov, 1962b, 1963; Monchadskii, 1950; Shvanvich, 1949; Wigglesworth, 1933a, 1933b; and others).

*Stadial (instar-wise) differences**.* A study of the preimaginal phases of Culisetina provided adequate material with which to describe the stadium-wise larval transformations of only 6 species. Three of these species belonged to subgenus *Culiseta* s. str. (*C. alaskaensis indica*, *C. annulata subochrea* and *C. bergrothi*), two to the subgenus *Culicella* (*C. morsitans morsitans* and *C. silvestris amurensis*) and the last one to *Allotheobaldia longiareolata*. Thus, the main Palaearctic groups of Culisetina are fully represented.

It is easy to differentiate the 1st instar larvae from the other more mature ones***; in all species of Culisetina as in most other Culici-

*Gill index represents the ratio of the length of gills to the length of the anal segment.

**Here, as elsewhere in this work, the adjective "stadial" derived from the word "stadium" and not "stagewise" has been used. This has been done to avoid possible misunderstandings since in the last few decades the words "stagewise development" and others have been used extensively to describe the interrupted stages in the development of some plants. The author has used "stadial" ("stadium-wise transformations" and other similar words) to describe the transition from one stadium to another within the larval stages of an insect.

***To avoid cluttering up the text with numerical data, only one table has been given, Table 4, showing the stadiumwise larval differences as in *C. bergrothi*.

nae, the egg tooth is distinctly visible and the ventral brush is absent. Moreover, the 1st instar larvae of all Culisetina have less distinct chaetotaxy: many setae on the head and the posterior end of the body are simple and single, while they are branched in the 2nd and subsequent stages (Table 4). The 1st instar larvae also differ in dimensions. This factor is very convenient in distinguishing all stages in live material as Table 4 indicates. An excellent additional feature permitting the differentiation of the first instar larvae of all members of the genus *Culiseta* is the distinct separation of primary and secondary sclerotization of the siphon (Fig. 49). This feature is not, however, applicable to the larvae of *Allotheobaldia longiareolata* since such a distinction of siphon sclerotization is often seen in their 2nd instar.

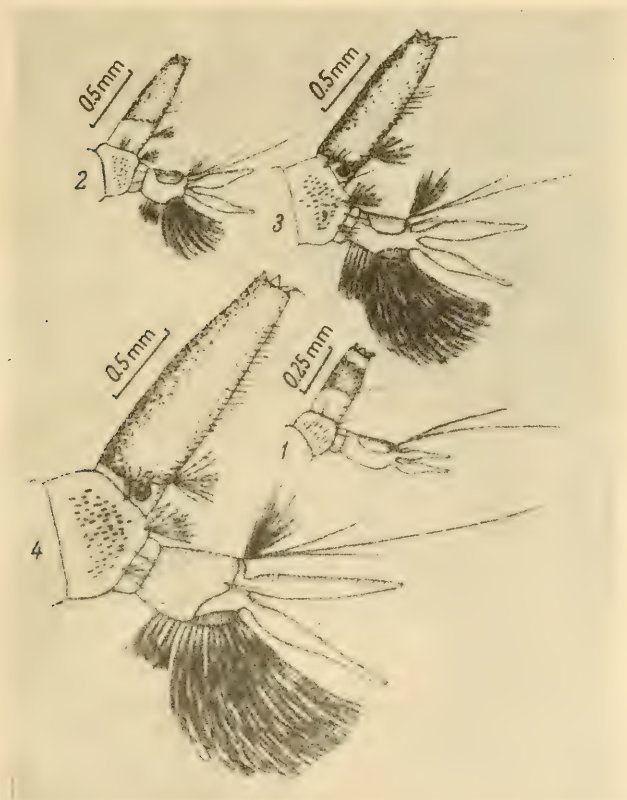
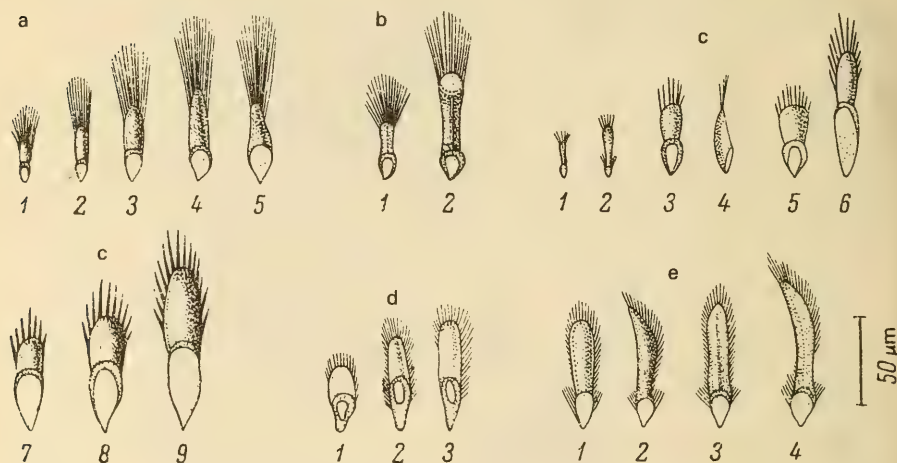


Fig. 53. Posterior end of the body in all larval stages (1-4) of the mosquito *Culiseta bergrothi*.

Even the differentiation of 4th instar larvae poses no difficulty. In all members of the subtribe Culisetina, except *A. longiareolata*, there is an annular ring completely surrounding the anal segment (Fig. 53 and Table 4). In the 4th instar larvae of Culisetina, all the skeletal structures and such structures as the comb of segment VIII (Fig. 54), siphon crest and others are highly developed (Table 4). The increasing differentiation of the ventral brush in the course of 78 stadium-wise transformations is interesting. It is absent in the 1st instar larvae and later an increase in the number of setae set on the common base was apparent from stadium to stadium; simultaneously, there is a reduction in the number of setae set anteriorly to the common base of the ventral brush (Table 4).

The differentiation of the 2nd and 3rd larval instars usually poses the greatest difficulty. For this purpose, the variational series were compared and Fisher's reliability criteria calculated for most morphological factors studied. The results of these investigations (Maslov, 1963) suggest that the absolute body dimensions (head and siphon length) in all six species studied represent a good differential and diagnostic feature permitting the differentiation of the 2nd and



80

Fig. 54. Comb scales in some members of Culisetina.

a—4th instar larva of *Culiseta morsitans morsitans*; b—4th instar larva of *C. silvestris silvestris*; c—larva of *Allotheobaldia longiareolata*; d—4th instar larva of *Culiseta bergrothi*; e—4th instar larva of *Culiseta silvestris amurensis* (d and e—after Monchadskii, 1947). 1 and 2—larvae of the 1st stage; 3 and 4—2nd instar larvae, dorsal and lateral views; 5 and 6—3rd instar larva; 7-9—4th instar larvae.

- 3rd larval instars and the number of comb scales on segment VIII (Table 5). The extent of branching of setae on the head is not always a reliable criterion in this respect. While branching of the antennal seta (Table 5) permits excellent differentiation of the 2nd and 3rd larval instars in *Culiseta subochrea*, *C. morsitans* and especially in *C. silvestris amurensis*, it is less reliable for *C. alaskaensis indica* and *Allotheobaldia longiareolata* and is totally inapplicable for *Culiseta bergrothi*. The branching of the outer frontal seta (Table 5) permits an objective evaluation of differences between the 2nd and 3rd larval instars only in *C. alaskaensis indica* and *C. annulata subochrea*.
- 80 Other setae on the head (as Table 4 indicates) provide even less data on which to differentiate the 2nd and 3rd larval stages. In some cases, we used such factors as the branching of the siphon seta (*Culiseta annulata subochrea*, *C. silvestris amurensis* and *Allotheobaldia longiareolata*), nature (microstructures) of the sclerotization of the saddle (*A. longiareolata*), the number of teeth on the siphon crest (*C. alaskaensis indica*, *C. bergrothi*, *C. morsitans* and *C. silvestris amurensis*) and others. Vital stadium-wise transformations were noticed in the character of mouth parts which has been discussed
- 81 above. On the other hand, some morphological indices (for example, the head index, number of ventral brush setae on the common base and anterior to it, and many others, Table 4) were found to be totally unsuitable.

79 **Table 5. Comparison of some morphological characteristics of the 2nd and 3rd instar larvae**

Characteristic	Second instar larvae		Third instar larvae		t
	Range	Mean	Range	Mean	
<i>Culiseta alaskaensis indica</i> Edw.					
1. Branching of antennal seta	2-7	4.2	4-10	6.5	9.5
2. Branching of outer frontal seta	3-7	4.2	5-10	7.3	12.3
3. Number of scales on comb	15-30	20.3	20-40	30.8	11.5
4. Number of ventral brush setae anterior to common base	6-9	7.0	4-7	5.8	6.8
5. Branching of siphon seta	2-4	2.9	3-6	4.4	9.7
6. Number of teeth on crest	5-10	7.2	7-13	10.1	10.7
<i>Culiseta annulata subochrea</i> Edw.					
1. Branching of antennal seta	2-7	4.4	5-10	7.4	10.7
2. Branching of outer frontal seta	3-6	4.0	5-10	6.6	10.9

(Contd.)

Characteristic	Second instar larvae		Third instar larvae		t
	Range	Mean	Range	Mean	
3. Number of scales on comb	15-30	20.9	25-45	38.3	21.2
4. Number of ventral brush setae anterior to common base	2-8	6.1	4-7	4.9	6.6
5. Branching of siphon seta	2-4	2.9	4-7	5.4	14.5
6. Number of teeth on crest	5-11	8.2	6-14	9.2	2.8
<i>Culiseta bergrothi</i> Edw.					
1. Branching of antennal seta	4-9	5.6	4-9	6.0	3.3
2. Branching of outer frontal seta	4-7	4.8	5-10	6.5	15.4
3. Number of scales on comb	25-55	40.0	55-75	64.9	24.2
4. Number of ventral brush setae anterior to common base	6-10	8.2	5-9	7.0	10.6
5. Branching of siphon seta	2-5	3.4	3-6	4.6	9.3
6. Number of teeth on crest	6-10	7.7	6-14	12.0	32.9
<i>Culiseta morsitans morsitans</i> Theo.					
1. Branching of antennal seta	5-10	7.5	10-23	17.3	11.8
2. Branching of outer frontal seta	2-5	3.0	2-6	3.9	3.3
3. Number of scales on comb	50-80	66.3	70-110	91.8	9.1
4. Number of ventral brush setae anterior to common base	7-9	8.0	6-8	7.1	5.4
5. Branching of siphon seta	2-4	2.5	3-5	4.1	7.1
6. Number of teeth on crest	3-6	4.5	6-11	7.6	8.2
<i>Culiseta silvestris amurensis</i> Masl.					
1. Branching of antennal seta	5-11	8.5	16-28	22.2	29.3
2. Branching of outer frontal seta	1-4	2.5	2-7	4.1	8.2
3. Number of scales on comb	20-40	30.3	35-75	52.3	13.5
4. Number of ventral brush setae anterior to common base	6-9	7.5	6-8	7.1	2.8
5. Branching of siphon seta	2-4	2.8	4-6	5.1	16.5
6. Number of teeth on crest	3-7	5.1	6-10	8.1	12.3
80 <i>Allotheobaldia longiareolata</i> Macq.					
1. Branching of antennal seta	1-2	1.3	2-3	2.2	9.9
2. Branching of outer frontal seta	1-2	1.4	1-3	2.1	5.7
3. Number of scales on comb	15-25	19.3	25-35	31.5	17.2
4. Number of ventral brush setae anterior to common base	5-8	6.4	4-7	5.2	6.9
5. Branching of siphon seta	2-4	3.0	5-8	6.4	19.9
6. Number of teeth on crest	3-8	6.2	6-14	8.7	9.5

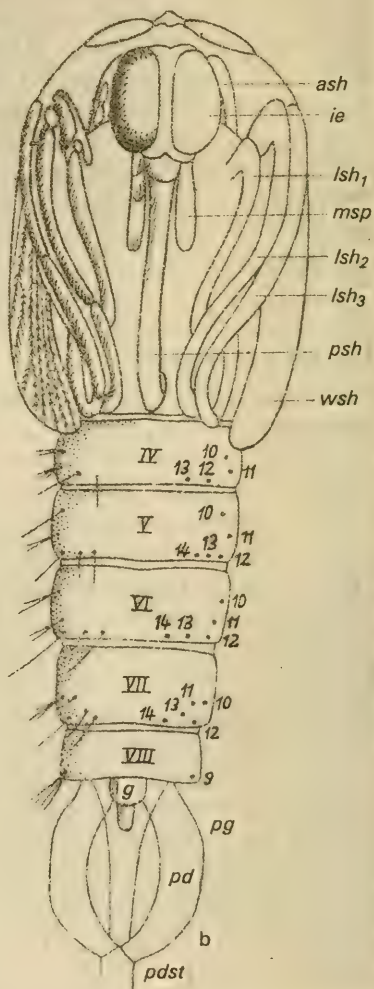
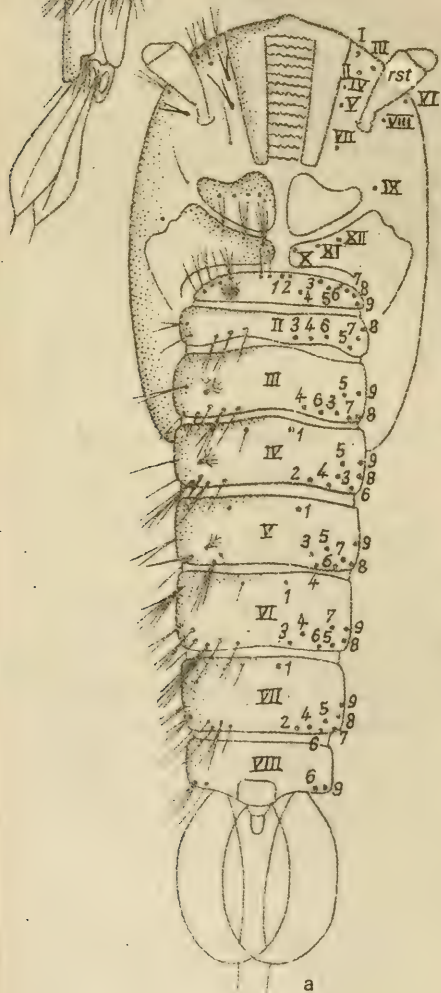
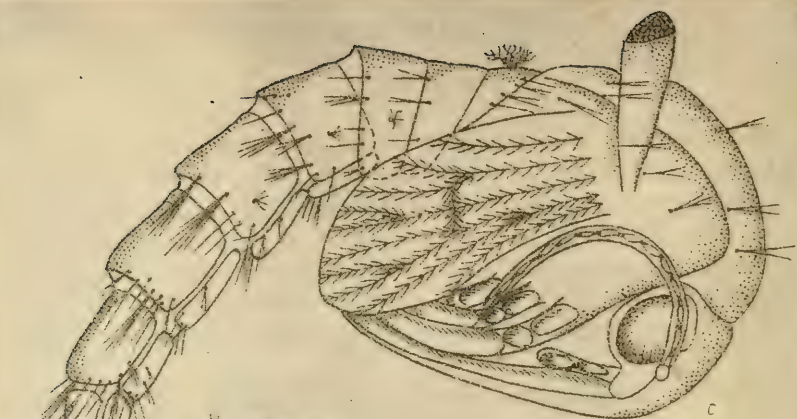
Note: Fisher's reliability criterion: $t = (M_3 - M_2) / \sqrt{m^2_3 + m^2_2}$ — (Indices at M and m denote the larval stadia).

Pupa

There are very few differences in the structure of the pupa of Culicidae and Culisetina. The body of the pupa can be separated into two distinct sections: the cephalothorax and the abdomen consisting of eight normal and two (IX and X) modified segments and the paddle (nageoire, paddle, fin, Ruderplatten, others) joined to segment VIII (Fig. 55a, b, and c). A groove separating the head case from the thorax is distinctly visible in the cephalothoracic portion (Fig. 55, c).

In freshly molted pupae, the integument is pale and gradually sclerotized and the developing imaginal structures are visible. The sheaths of imaginal appendages (antennae, proboscis, palp, wings and legs) (Fig. 55b and c) are easily distinguished 36-48 hr after molting in *Culiseta bergrothi* at a mean temperature of +15-18° C and in *C. alaskaensis alaskaensis* at +16° C. Also distinctly manifested are such specific characteristics of the species as the annulations of the tarsal segments, wing pads and especially the structure of the male hypopygium. A broad medial ribbed zone is clearly visible on the dorsal surface of the cephalothoracic shield in *Culisetina* pupae (Fig. 55a). Two plates usually homologous with metathoracic sclerites and two others anterior to them are clearly seen along the posterior dorsal region (Fig. 55a). Paired respiratory trumpets are found dorsolaterally. While examining the association of respiratory trumpets and the original tracheal trunks of pupae with the imaginal respiratory organs, it can be seen that this association with the anterior imaginal spiracles is similar to the one shown by Roddy (1955) for the pupal respiratory trumpets with the prothoracic stigmata in *Ophyra aenescens* Wied. (Diptera, Muscidae).

By comparing differences in relative length, width and nature of sclerotization of respiratory trumpets in different species, attempts have been and are being made by some scientists (Chinaev, 1939, 1945; Rioux, 1958; Senevet and Andarelli, 1959a; Volkova, 1962) to use these structures as factors of taxonomic significance. For example, in the identification tables of Senevet and Andarelli (1959a) (p. 237), the main difference between the pupae of *Culiseta glaphyrop-tera* and *C. annulata* (and *C. subochrea*) is that in the former species the ratio of the length of the respiratory trumpet to that of the fin [paddle] was 2:3.5 (=0.57) and in the latter two, 2.5:4 (=0.63). A comparison of these numerical values indicates that the differences are so minute that errors do occur while measuring the lengths of the trumpets and paddles. Moreover, the author's measurements of



these organs (Maslov, 1963) show that in the pupae of four species (and one subspecies) the ratio of the length of the respiratory trumpet to that of the paddle (index of the relative length of the respiratory trumpet) cannot be regarded as constant for each species, but is subject to fairly significant variations. There are similar findings for the other index characterizing the form of the respiratory trumpet, that is, the ratio of the maximum diameter of the apical opening to the length of the trumpet (index of the form of the respiratory trumpet).

The chaetotaxy of the cephalothorax is rather sparse: there are three pairs of setae (I-III) in the head section; setae IV-IX are on the pro- and mesothoracic sections; of these, seta VIII is found anterior and seta IX posterior to the respiratory trumpet; the last three pairs of setae (X-XII) are found on the metathoracic lobes. There are 83 differences in the extent of branching of the cephalothoracic setae in different species, but they are not adequate for extensive use in systematics. Moreover, it is difficult even to detect the cephalothoracic setae in the darkly pigmented pupae (except the clearly visible setae X-XII of the metathorax).

Eight tergites (Fig. 55a) are clearly visible above the abdominal section along with the modified ninth (*g*—genital) and tenth (*pg*) segments. The first sternite is absent in the ventral sclerotization. The second as well as the third sternites are usually obscure on the dorsal surface under the large cephalothorax; thus, only the 4th to the 8th and the genital sternites are visible from below (Fig. 55b). However, in cleared specimens, deep median sclerotization of the anterior sternites is distinct in the abdomen, separate from the cephalothorax or in the molten cuticle exuviae. The anteromedian lobe of the third sternite is especially heavily sclerotized; it is the one most anteriorly extended. Somewhat less sclerotized and more uniformly rounded is the fourth sternite, followed by the second; the anteromedian sclerotization of the fifth sternite is comparatively

Fig. 55. Structure of pupa.

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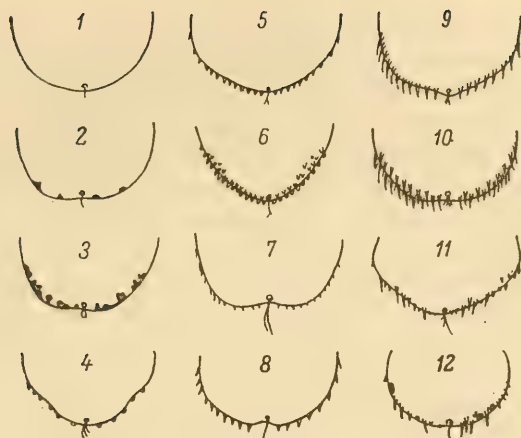
a—dorsal view above; *b*—ventral view; *c*—lateral view. Left of *a* and *b* chaetotaxy in the pupae of *Culiseta bergrothi* is shown and on the right the enumeration of setae. The Roman numerals represent the numbers of the abdominal segments and, on the cephalothorax, the numbers of setae. *ash*—sheath of imaginal antenna; *ie*—imaginal eye; *lsh*₁, *lsh*₂, *lsh*₃—sheaths of imaginal legs; *psh* and *msh*—sheaths of proboscis and maxillary palp in female; *wsh*—wing sheath; *rst*—respiratory trumpet of pupa; *g*—genital (IX) segment; *pg*—postgenital (X) segment; *pd*—paddle; *pdst*—paddle seta.

weakly developed. At least, such a pattern has been noticed in investigations on the pupae of 6 species of *Culisetina* studied for this purpose.

On the normal abdominal segment we find 14 pairs of setae of which the first 5 or 6 occupy the dorsal position, the next 4 or 5 setae are located laterally and there are 4 ventral setae. On the first segment, in which the sternite is absent, there is a maximum of only 10 setae (Fig. 55a). This is also on the second segment in which the sternite is present but devoid of setae. Among the setae of the first segment we clearly see the dendritic seta 4 (Fig. 55a) functioning as a suspensory structure and as a sensory apparatus responding to the vibrations of the water surface. Other setae of the first and other segments could be long (when their length is similar to that of the segment or exceeds it), short or rudimentary; they may be single, two-, three- or several-branched or split at the apex and so on. All of them vary widely not only in each species, but on the right and left sides of even the same pupa and hence the chaetotaxy can be used in the systematics of *Culisetina* only as a supplementary feature.

The paddle attached to the eighth segment is in the form of two fairly broad, usually irregularly oval, plates. The ratio of length to width of the paddle expressed as a percentage and called by the author the index of paddle form, varies over a wide range, but can be considered an additional feature of taxonomic importance. In particular, as several investigators noted (Chinaev, 1945; Kirkpatrick, 1925; Rioux, 1958; Senevet and Andarelli, 1959a), the values of this index for the pupae of *Allotheobaldia longiareolata* usually slightly exceeds 100% while, with rare exceptions, it is over 125% for species of the genus *Culiseta*.

The investigations of Peus (1930a) revealed the differences in the nature of the marginal crenation of paddles in the pupae of *Culiseta annulata* and *C. subochrea*: bluntly rounded and placed in two rows in the former and sharply pointed in the latter. Rioux (1958) and Senevet and Andarelli (1959a) later stated that this difference is far from absolute, since the pupae of *C. annulata subochrea* often have a paddle crenation of the type "annulata" and, on the contrary, the pupae of *C. annulata annulata* have sharp paddle crenations. A similar diversity in the nature of the microscopic structure of the paddle margin has also been found in the author's material. In particular, 85 these types, with both sharp and blunt crenations with transitions between them, were seen among the pupae of *C. alaskaensis* and *C. bergrothi* (Fig. 56, 6 and 10). In the former, pupae with a paddle totally devoid of crenation (Fig. 56, 2 and 3) were seen which, at least



84 Fig. 56. Types (1-12) of rear margin of the paddle lobe in pupae.

in the author's material, was characteristic of the pupae of the species of the subgenus *Culicella*. These features of paddle structure are associated with ecological conditions. The structural diversity of the paddle margin is shown in Fig. 56 (1-12).

The paddle seta varies in relative length and branches along the median posterior margin of each paddle lobe (Fig. 56, 1-12). In some cases, these differences could be of specific taxonomic importance. For example, the paddle seta is absent in the pupae of *Theomyia fraseri* (Van Someren, 1956); it is very strong and hook-shaped in *C. glaphyroptera*, relatively weak and generally simple in *C. bergrothi* (also in *C. litorea*) and so on. However, even here, the taxonomic importance of this feature should not be overemphasized.

As mentioned above, in mature pupae, the imaginal structures are easily visible through the thin integument on the pupal sheath and can be used to determine specific characteristics. In field work, male pupae in particular can be differentiated this way, since the pupal characteristics in most cases are extremely unreliable due to their variability.

Biology

Regional adaptations: Although Culisetina mosquitoes are distributed almost all over the world, they cannot be classed as common or widespread species. However, scientists have more frequently encountered mosquitoes of this group in certain cases. In particular, Kh.Ya. Remm (1955, 1957) noted that *Culiseta alaskaensis* constituted 1.8% in Estonia, while Stage and Chamberlain (1945) encoun-

tered this species in Alaska to the extent of 10.7%. Sicart and Escande (1958) described massive attacks on men by *C. annulata* in Toulouse; Harmston and Rees (1946) described *C. incidens* as one of the most widespread mosquitoes (18%) in Oregon and so on.

Based on the frequency of encounter in different topographic zones, mosquitoes can be classified into three groups: mosquitoes of the forest zone, forest-free areas and human habitations.

The lone representative of *Culisetina* developing only in tree holes, the African *Theomyia fraseri* (Garnham et al., 1946, in Kenya; Haddow et al., 1951 in Uganda; Rageau and Adam, 1952 in Cameroons), should be included among the specific forest inhabitants. Most of the species of the subgenus *Neotheobaldia* and *Culiseta* (*Culicella*) *inconspicua* and *Austrotheobaldia littleri* are among the forest-associated species confined mainly to the hilly-forest landscapes; they are the causative forms of Australian endemics*, at least those species encountered in Victoria and whose ecology is known (Dobrotworsky, 1954, 1960). Only the last of these is occasionally found in Victoria outside the forested regions. *C. glaphyoptera*** is an inhabitant of the hilly forests of Rumania (Apfelbeck, 1928), Bulgaria (Bozhkov, 1959), Czechoslovakia (Kramář, 1958), and so on. There are similar data on *C. kanayamensis* in northeastern China (Ch'in, 1959). Although *C. alaskaensis alaskaensis* and *C. bergrothi* are mostly associated with the forest areas in all zones of their extensive ranges (Gutsevich, 1939, 1947, 1953; Jenkins, 1948; Jenkins and Knight, 1950, 1952; Kramář, 1958; Maslov, 1963; Petrishcheva, 1947; Rempel, 1950; Rumsh, 1948; Volozina, 1961), they are also often encountered in the open forest-free landscapes (Table 6) and even in the human environment. Remm (1955, 1957) pointed out that the larvae of *C. alaskaensis* were encountered in Estonia in water reservoirs in the forest and forest-free zones while the adult forms were caught more often in the villages. This was also reported by Skierska (1955) in Poland; Natvig (1948) noted that in West and East Germany, *C. alaskaensis* was found mostly in sparse forests and to the north, in Norway, in forest-free regions. *C. bergrothi* breeds in forests almost as well as in forest-free regions of Norway and up into the mountains at heights of 620 m (Natvig, 1948). According to the author's observations, it was also found in the Far East (Table 6).

*Certain Australian species are considered to be serious biting pests of humans, but are not involved in the transmission of pathogens [Editor].

**The references in literature to the presence of *C. glaphyoptera* in the forest-free zones, especially in the Far North, are erroneous and evidently pertain to another species, *C. bergrothi*.

In North America, *C. alaskaensis* also occurs in the forest regions of Alaska (Frohne, 1954a; Jenkins, 1948) and Canada (Jenkins and Knight, 1952; Rempel, 1950). *C. impatiens* is also found in the forests (Boddy, 1948; Frohne, 1953; Rempel, 1950, 1953, and others); this species is found in the hills at heights greater than those of most other *Culiseta*, up to 2,000 m in Quebec (Jenkins and Knight, 1950) and even 2,900 m in Colorado (Dyar, 1924b).

The main forest inhabitants among the members of the subgenus *Culicella* are the mosquitoes *Culiseta morsitans* in Eurasia and in North America. There are few references in literature to the occurrence of this species outside the forest zone. Goetghebuer (1910) stated that *C. morsitans* was found everywhere, even in the hills. Aitken (1942) [1954] mentioned that this species lives in the open regions of Corsica. Other scientists have reported this species in other regions (Headlee, 1945 for New Jersey; Jenkins and Knight, 1952 for Ontario; Séguy, 1924, 1925 for North Africa and France, and others).

Among the other members of the subgenus *Culicella*, a predominantly forest distribution is typical of Australian *Culiseta inconspicua* (Dobrotworsky, 1954), of Ukrainian *C. ochroptera** (Val'kh, 1957, 1959) and of Crimean *C. setivalva* (Velichkevich, 1931, 1936).

C. inornata and *C. melanura* are among the mosquitoes recorded from the forest and open regions of North America.

The more specific inhabitants of open territories, found only rarely in forests and breeding in water reservoirs in the forests, are *C. annulata annulata* in the Old World and *C. incidens* in North America. In several works devoted to the ecology of *C. annulata*, its distribution has been reported as confined to the exposed open plain 86 biotopes and the species has been cited as a forest dweller in only very few instances. This species has been identified often, even in the hilly regions: Pirumov and Ananyan (1935) and Nagiev (1961) found it in the hills of Armenia and Azerbaijan at heights up to 1,200 m; in Czechoslovakia, Kramář (1958) found it at heights up to 1,000 m; Natvig (1948) reported it in northern Europe at 520 m and Stovbun (1956) recorded this species (and *C. alaskaensis*) from Stanislav region as a specific inhabitant only of lowlands.

C. incidens, which is common in the open plains of the USA and Canada, has been reported in forests in Washington (Boddy, 1948), in the northwestern states on the Pacific coast (Yates, 1953) and from a few other sites.

Among the mosquitoes of the subgenus *Culicella*, the Far Eastern *Culiseta silvestris amurensis*, could be placed in this group. Its presence in the forest-free biotopes of Primorye and northeastern

*This reference apparently pertains to the mosquito *Culiseta silvestris silvestris*.

Table 6. Regional adaptations of the Far Eastern members of the genus *Culiseta*

[Location]	Region	Taiga section		Sparse taiga		Shrubbery sections		Wet meadows	
		Caught	Bites	Caught	Bites	Caught	Bites	Caught	Bites
<i>Culiseta alaskaensis alaskaensis</i> Ludl.									
Shilki River basin, 1934 and 1935	Hilly	1.07	0.15	1.05-	0.16	0.02	0.05	0	0
	Plain	0.47	0.06	0.44	0.09	0.11	0	0	0
Amguni River basin, 1931									
<i>Culiseta bergrothi</i> Edw.									
Shilki River basin, 1934 and 1935	Hilly	1.81	0.37	1.76	0.43	0.92	0.19	0.07	0
	Plain	3.67	0.54	2.59	0.40	2.21	0.14	0.22	0
Amguni River basin, 1931	Hilly	3.00	0.47	—	—	0.89	0.13	0	0
	Plain	6.6	0.06	—	—	0.11	0	0	0
Khora River basin, 1946	Hilly	3.5	0.24	—	—	—	—	2.2	0.27
	Plain	0	0	—	—	—	—	0	0
Bikina River basin, 1933	Hilly	2.61	0.52	—	—	2.25	0.37	0.23	0.05
	Plain	0.30	0.04	—	—	0.15	0.02	0	0
<i>Culiseta sibirstris amurensis</i> Masl.									
Khora River basin, 1946	Hilly	0	0	—	—	—	—	0	0
	Plain	0.8	0	—	—	—	—	0	0.05
Bikina River basin, 1933	Hilly	0	0	—	—	0	0	0	0
	Plain	0	0	—	—	0.22	0	0.29	0.01

Note: The figures given everywhere are for relative imaginal abundance: $0=k/u$, where k is the number of mosquitoes of a given species and u —the total number of all mosquitoes counted.

China was reported by Petrishcheva (1947, 1959), Ch'in and Su (1959) and Ch'in (1959) and in the forest regions by Monchadskii (1947) and P.A. Petrishcheva (1951). In southern Amur, they are mainly confined to the forest-free regions (Table 6) although, as the Table indicates, they are occasionally caught even in the taiga zone. Table 6 indicates that, in the same landscape and climatic zone, the frequency of relative abundance of mosquitoes depending on the topography is far from identical. On the other hand, under similar relief conditions, the relative abundance of a species varies with the climatic conditions. Thus, in the basin of the River Khungari, the mosquito *C. bergrothi* is a common species in the hilly-taiga biotopes (500–600 m height), but it is found even more often in the taiga plains. A frequent companion of the mosquito in the forest-free shrubbery zone of the Khungari River basin hills, *C. bergrothi* is rare in similar shrubbery growths in the plains. Farther southward, this species is increasingly confined to the hilly taiga massifs (Khora and Bikina River basins; Table 6). On the contrary, *C. s. amurensis* is not found in the hilly area of the Amur region. All other species of Culisetina mosquitoes for which even scanty information is available on their range of distribution fall in the group of specific inhabitants of the plains. Among them are most of the representatives of the subgenus *Culicella*: *C. fumipennis*, *C. litorea*, *C. silvestris ochroptera* and *C. minnesotae*. The first three are found mostly in the plains or in deep valleys and *C. minnesotae* is found fairly high in the hills; it has been found in Utah at heights of 1,500 m (Nielsen and Rees, 1959). *C. annulata subochrea*, *C. alaskaensis indica*, *C. niveitaeniata* and *C. particeps* of the subgenus *Culiseta* s. str. have not been reported in the forest biotopes.

Allotheobaldia longiareolata is also not known in the forests. This typical species is found in hilly regions at greater heights than all other representatives of Culisetina: in the Caucasus, Pirumov and Ananyan (1935) found it at heights of 1,190 m and Nagiev (1961) reported it at a height above 2,000 m. It has been reported in Syria and Palestine at 1,350 m (Barraud, 1920), in Yemen up to 1,500 m (Knight, 1953), in Eritrea up to 2,480 m (Lewis, 1943) and in the Sierra Nevada region (in August 1954) up to 3,000 m (Rioux, 1958).

Among these mosquitoes, *Culiseta glaphyroptera*, *C. impatiens*, *C. niveitaeniata*, *C. litorea*, *C. inconspicua*, *C. morsitans dyari*, *C. setivalva*, *C. silvestris silvestris*, *C. silvestris ochroptera*, *C. s. amurensis*, Australian Culisetina and African *Theomyia fraseri* have not been reported from human habitations.

Some other species are found in cultivated landscapes. Among them, Skierska (1955) reported *C. alaskaensis* as a house-dwelling

mosquito in Poland, while Zvyagintsev (1946) found *C. indica* in human habitations in Kabarda and E.M. Lavrenko (1953) in Ismail.

87 *C. bergrothi* has been found in cultivated landscapes by Natvig (1948) in northern Europe and by Petrishcheva (1947) in the Far East; *C. ornata* has been reported as a domestic inhabitant by Cockrell (1913) and by others in Colorado, by Ripstein (1935) in Mexico, by Rempel (1953) in Saskatchewan and by Yates (1953) in the northwestern states on the Pacific coast. Under man-made conditions *C. morsitans morsitans* was found by Zabud'ko-Reingard (1937) in Abkhaz and by McGregor (1921) in England. American investigators reported *C. melanura* in Virginia in cultivated areas.

Among mosquitoes for which cultivated fields are the usual habitats, only *C. annulata annulata* and *Allotheobaldia longiareolata* can be cited in the Old World and *C. incidens* in North America. The former is often also called a domestic mosquito. The references of several investigators (Rioux, 1958) to the exceptional exophily of *C. annulata subochrea* have evidently been exaggerated: this mosquito is known from human habitations in Central Asia and Kazakhstan (Kazantsev, 1932, 1936; Petrishcheva, 1936, 1954 and several others), in Corsica (Aitken, 1942) and in Poland (Skierska, 1955).

Summarizing the information available in literature, all Culisetina mosquitoes can be grouped as shown in Table 7 according to their regional adaptations.

89 *Biotopes of preimaginal phases:* An overwhelming majority of Culisetina fall within the category of eurytopic species. *Allotheobaldia longiareolata* and the two subspecies of *Culiseta annulata* have the widest range of possibilities in this respect. These two species were recorded from water reservoirs of various dimensions, depths, degrees of stability, chemical conditions, putrefaction, thermal range, shaded conditions, growth of water vegetation and other factors. The following species also exhibit significant eurytopicity: *C. alaskaensis* (with the subspecies *indica*), *C. bergrothi*, *C. impatiens*, *C. incidens* and *C. inornata*; and among the species of the subgenus *Culicella*, *C. morsitans* (with the subspecies *dyari*) and probably all the subspecies of *C. silvestris* and *C. melanura*. Other species have limited possibilities, which are evidently responsible for their relatively rare occurrence. Among them, *C. glaphyroptera*, confined to some rather small hills, is a fairly regular inhabitant of fresh-water reservoirs fed by hypothermal springs (Apfelbeck, 1928; Kramăr, 1958; Martini, 1929-31; Natvig, 1942; Peus, 1930b). In its requirements, *Culiseta kanayamensis* is close to *C. glaphyroptera* (Ch'in, 1959; La Casse and Yamaguti, 1950; Liu and Feng, 1956) and to *C.*

Table 7. Regional adaptation of the mosquitoes of subtribe Culisetina

	Forest	Predominantly forest	Predominantly plain	Plain
Conditions of vertical zoning				
Hilly	<i>Culiseta glaphyoptera</i> , <i>C. drummondi</i> , <i>C. hilli</i> , <i>C. frenchi</i> , <i>C. sylvanensis</i> , <i>C. victoriensis</i> , <i>Austrotheobaldia littleri</i>			<i>Culiseta niveitaeniata</i> , <i>C. silvestris minnesotae</i>
Hilly-plains	<i>Culiseta kanayamensis</i> , <i>Theomyia fraseri</i>	<i>Culiseta alaskaensis</i> <i>alaskaensis</i> , <i>C. bergrothi</i> , <i>C. impatiens</i> , <i>C. inconspicua</i>	<i>Culiseta annulata annulata</i> , <i>C. inornata</i>	<i>Allotheobaldia longiareolata</i>
Plains		<i>Culiseta morsitans morsitans</i> , <i>C. morsitans dyari</i> , <i>C. setivalva</i> , <i>C. silvestris</i> <i>silvestris</i> , <i>C. melanura</i>	<i>Culiseta incidens</i> , <i>C. silvestris amurensis</i> , <i>C. melanura</i>	<i>Culiseta alaskaensis indica</i> , <i>C. annulata subochrea</i> , <i>C. particeps</i> , <i>C. fumipennis</i> , <i>C. litorea</i> , <i>C. silvestris ochroptera</i>
Human associations				
Often			<i>Culiseta annulata annulata</i> , <i>C. incidens</i>	<i>Allotheobaldia longiareolata</i>
Random		<i>Culiseta alaskaensis alaskaensis</i> , <i>C. bergrothi</i> , <i>C. morsitans morsitans</i>	<i>Culiseta inornata</i> , <i>C. melanura</i>	<i>Culiseta alaskaensis indica</i> , <i>C. annulata subochrea</i> , <i>C. particeps</i>
Absent	<i>Culiseta glaphyoptera</i> , <i>C. kanayamensis</i> , <i>C. frenchi</i> , <i>C. hilli</i> , <i>C. victoriensis</i> , <i>Austrotheobaldia littleri</i> , <i>Theomyia fraseri</i>	<i>Culiseta impatiens</i> , <i>C. inconspicua</i> , <i>C. morsitans dyari</i> , <i>C. setivalva</i> , <i>C. silvestris silvestris</i> , <i>C. melanura</i>	<i>Culiseta silvestris amurensis</i>	<i>Culiseta niveitaeniata</i> , <i>C. fumipennis</i> , <i>C. litorea</i> , <i>C. silvestris minnesotae</i> , <i>C. silvestris ochroptera</i>

Note: Ecological data are not available for *Culiseta atlantica*, *C. atra*, *C. nipponica*, *C. antipodea*, *C. otuayensis*, *C. weindorferi*, *C. tonnoiri*.

niveitaeniata (Barraud, 1924; Liu and Feng, 1956; Myn Tsin-Khua, 1955). Also interesting are such extreme stenotopic species as the inhabitants of tree holes, the Central African *Theomyia fraseri* and the Australian *Culiseta drummondi*, *C. frenchi*, *C. hilli*, *C. sylvanensis* and *C. victoriensis*. Their specific biotopes, the tunnels made by land crayfish (*Eugaeus*) and the deserted burrows of wombats (Dobrotworsky, 1954, 1960) specifically influence some morphological features of these species (faint pigmentation) and their behavior.

A lengthy study of the ecology of Culicidae in the Far East led to a detailed analysis of the conditions of the natural habitat of the preimaginal phases of three Far Eastern species of *Culiseta* for which significant ecological adaptability has been noticed (Maslov, 1963).

Each species has its own optimal conditions. These conditions are nearly identical for the two species of the subgenus *Culiseta* s. str., *C. bergrothi* and *C. alaskaensis alaskaensis*. The preimaginal stages of these mosquitoes are usually found in small (area of water surface up to 1–2 m²) but deep or moderately deep (over 50 cm) water pools. Such pools usually have an underground water source, although in the spring are often fed by snow and in the summer by floods. There is invariably no flow and the water is fresh; often *C. bergrothi* is found in weakly saline springs with a salt content up to 400 mg liter; the pH of the water varies widely from 5.8 to 8.6; usually the water is β -mesosaprobic, more rarely α -mesosaprobic and very rarely oligo- or polysaprobic. During a season, a successive variation of putrefaction in an extremely wide range is seen in a given reservoir with mosquito larvae and pupae. The thermal range in the southern regions is predominantly hypothermal; in the north, it is hyper- or isothermal with almost constant shade over the water surface (in the south) or its absence (in the north). The growth of submerged and floating vegetation is usually little or nil. Furthermore, in northern areas (Chukotka, Kolyma, others) the optimum temperature is never the same as in the southern zones (central Amur, Primorye and others).

Totally different growth conditions are typical of the preimaginal stages of *C. silvestris amurensis*: water reservoirs of moderate size (200–300 m²), fairly deep with an underground water source, stagnant or even slowly flowing water, invariably fresh, more often
90 oligo- or β -mesosaprobic, but not beyond. Isothermal conditions are rare, more often they are hyper- or hypothermal (in the spring and autumn). An abundant growth of submerged and floating vegetation is nearly always essential.

The life of individual mosquito larvae shows fairly diverse

behavioral responses varying in relation to environmental changes (Maslov, 1964b).

In a special series of experiments (Maslov, 1964b), the individual adaptability of larvae appeared to be associated with the development of temporary neural links enabling it to respond quickly to unfavorable external influences. The adaptive changes of behavioral norms are particularly distinctly manifested in relation to those environmental factors which keep changing in the common natural habitats of larvae. Examples of this include light intensity and slight disturbance of the water surface. In the larvae of *C. bergrothi* which have extensive feeding possibilities (filter feeding on plankton and scraping of periphyton), fairly rapid adaptive changes of behavioral norms are possible. The larvae can then more completely utilize the food resources while confined to any one of these foods (Maslov, 1955, 1961a, 1961e, 1964b). However, prolonged feeding of larvae (during the first three stages of larval development) under conditions restricted to one food type strengthens their response in a single direction so that the variability of the larval feeding behavior norm decreases sharply. Active selection of more favorable conditions has also been noticed in larvae of *C. bergrothi* in relation to light intensity, degree of development of floating vegetation, population density, temperature and others (Maslov, 1964b).

In the very highly specialized periphytophages, *C. annulata subochrea* and *C. alaskaensis indica*, the feeding habits of mature larvae (3rd and 4th instar) are less variable: here, unfavorable food restriction (exclusively to periphyton) in variably results in a gradual increase in restlessness and ultimately the death of all larvae (Maslov, 1955, 1961a). The results are different in the periphytophagic and predatory *Allotheobaldia longiareolata* under restricted feeding conditions: the fully grown larvae of this species (4th and to a smaller extent, the 3rd instar), starved from periphyton food, resort to predaceous habits and cannibalism. They also feed equally avidly on their own and other species; the rapid extinction of the larvae of other species in mixed populations of two species (*A. longiareolata*+*Culex pipiens*) is not because of their active selection by the predator nor its "repulsion" to feeding on its own species, but because of the greater access to the other larval species incapable of actively defending themselves (Maslov, 1955, 1961a, 1961e, 1963).

Like the differences within population (intraspecific) relations arising from differences in feeding variations, an experimental study showed that individual behavior and relations among specimens of a given species change in relation to population density. Thus, the larvae of *Culiseta bergrothi* under slightly overpopulated conditions

(population density 4–5 larvae or more per cm²), while moving from place to place in search of a more favorable environment, fight with each other. In this process, the older larvae usually gnaw at and chase the interlopers; no chemical (“teleorganic”) repellants were noticed in the author’s studies (*C. bergrothi*, *C. annulata subochrea* and *C. alaskaensis indica*) and no genuine cannibalism has been noticed in these two species, although there have been instances of biting each other and even (in the 4th instar larvae of *C. bergrothi*) feeding on the carcasses of dead relatives. In *A. longiareolata* larvae with predatory ability, we
 91 found distinct cannibalism under conditions of food scarcity. The result of intrapopulation differences of overcrowding in the first three species is the general reduction of the entire population and the survival only of a few members which are severely emaciated; the surviving population, thinned as a result of cannibalism, preserved its normal character including the vitality of these forms and the imago emerging from them.

Individual growth and life forms: The duration of growth of the preimaginal phases of Culicidae in the natural biotopes varies over a wide range as demonstrated by several investigators, especially in the case of *Culiseta* mosquitoes (Martini, 1929–31; Maslov, 1961c, 1962a, 1963; Wesenberg-Lund, 1920–21). Among the conditions determining the duration of growth and the course of metamorphosis, the effect of temperature is particularly important. This effect, in the author’s data, can be expressed in the form of Bodenheimer’s equation $S = K/(t - c)$ in which S is the duration of growth in days, K a constant calculated from Pierce and Blunk’s total heat equation $K = S(t - c)$, t the mean temperature in the growth period and c the critical minimum temperature calculated from Blunk’s equation:

$$\dot{c} = t_1 - \frac{S_2 (t_2 - t_1)}{S_1 - S_2}.$$

From study of the growth duration of *Culisetina* mosquitoes under different temperature conditions, we could deduce Bodenheimer’s equation for calculating the growth periods of *Culiseta bergrothi* mosquitoes and the two subspecies *C. annulata* and *C. alaskaensis* and *Allotheobaldia longiareolata* (Maslov, 1961c). It has been established that these equations are suitable only within an optimum temperature, with the boundaries specific for each species. At the same time, however, these are distinguishable for each species in different geographic zones. The latter factor limits the possibility of applying Bodenheimer’s equation deduced for some specific conditions to different climatic regions.

92 The stimulating effect of diurnal temperature variations, compared with a stable optimum temperature within the same limits and of a lower unfavorable temperature, was established by comparing the effects under different temperature combinations constituting a given mean growth temperature (Maslov, 1961c). High temperatures in a variable diurnal range exert an adverse, suppressive influence. While studying the cumulative effect of temperature and light, definite acceleration of the generations was noticed in *C. bergrothi* in the spring (gradual rise of temperature and prolongation of daylight) and their suppression in the autumn (lower temperature and shortening of daylight), compared with conditions of stable temperature and light, their mean values for the entire growth period remaining the same (Maslov, 1962a, 1963). In the larvae of euryphages (filter-feeding and scraping), restriction to one type of food did not affect the duration of growth while, in specialized scrapers, scarcity of food increased the period of metamorphosis. A similar inhibitive influence was invariably exercised by all other unfavorable and destructive external influences (Maslov, 1961c, 1962b, 1963).

As in investigations conducted on other subjects, more rapid growth and formation in males compared to females was noticed in *Culisetina* mosquitoes (Curtis, 1953; Dyar, 1916; McLintock, 1952; Maslov, 1961d; Theobald, 1904). Some males and females recorded significant variations in relation to growth conditions (Maslov, 1961d). However, the different ratio of males and females is explained not by the definitive influences of external agents (the formation of male or female reproductive glands is relevant in the 3rd and even in the 2nd instar larvae), but by the varying response to these factors (and varying vitality under given conditions) not only by adult males and females, but by male and female pupae and larvae (Maslov, 1960a, 1961d, 1963).

As demonstrated by many investigators (Danilevskii, 1956, 1961; Detinova, 1945; Hinton, 1953; Vinogradova, 1960, 1961), even in the case of *Culisetina* mosquitoes (Maslov, 1961b), the prediapause stage of hibernating female *Culisetina* mosquitoes is formed not in the adult members, but during preimaginal life under the controlling effect of autumn climatic conditions with endocrine and neural influences occurring during development of the larval and pupal phases. The dependence of prehibernation fat production in females upon reduction in the duration of daylight and corresponding temperature fall was experimentally established in three species of mosquitoes. The combined effect of daylight and thermal changes

on prehibernation fat production in females was studied in *Culiseta bergrothi* mosquitoes near Khabarovsk town and very high indices of correlation of the following three variables were obtained: degree of fat production, temperature and daylight duration during the growth of the preimaginal stages. The cumulative effect of daylight and temperature range on the formation of the prehibernation state is also confirmed by the fact that, under conditions of disturbed photoperiodism alone, neither the lowering of temperature nor the shortening of daylight had any perceptible influence on the degree of fat production in females.

The photothermal significance of prehibernation fat production in females is strong in all preimaginal stages, but the 4th stage larvae and pupae are particularly sensitive. Change in larval feeding alone does not exert direct influence on the degree of fat production of the females except that the quantitative inadequacy of the feed, like other unfavorable conditions, sharply reduces and sometimes even totally eliminates the effect caused by the lowering of temperature and shortened day.

Analysis of the data available in literature and the results of the author's investigations (Maslov, 1963) enable us to establish the following types, for *Culisetina* mosquitoes*.

I. Monocyclic with female diapause:

* <i>Culiseta glaphyoptera</i> **	— Central Europe
* <i>C. impatiens</i>	— Alaska, Canada
<i>C. alaskaensis alaskaensis</i>	— Alaska, Canada, Chukotka, northern Europe
<i>C. annulata annulata</i>	— Estonia, northern Scandinavia
<i>C. bergrothi</i>	— Chukotka, Taimyr, northern Urals
[<i>C. fumipennis</i>]	— northern Caucasus, North Africa

II. Polycyclic with female diapause:

* <i>Culiseta alaskaensis indica</i>	— Central Asia, Kazakhstan, Caucasus, Iran, Pakistan, India
* <i>C. particeps</i>	— southern states of the USA, Mexico

*Data are not available in literature for the classification of the following mosquitoes into one or the other type forms: *Culiseta atlantica*, *C. kanayamensis*, *C. niveitaieniata*, *C. atra*, *C. nipponica*, *C. drummondi*, *C. otwayensis*, *C. sylvanensis*, *C. weindorferi*, *C. antipodes* and *C. tonnoiri*.

**The species marked with an asterisk are those for which data on the types have been recorded only once. The species given within square brackets are those for which the data need confirmation.

- 93 **C. silvestris minnesotae* — USA
 **C. silvestris silvestris* — Ukraine
C. alaskaensis alaskaensis — central and eastern Europe, western Siberia, western Amur, Okhotsk coast
C. annulata annulata — northern and central Europe, Ukraine
C. annulata subochrea — northern and central Europe
C. bergrothi — Scandinavia, Amur, Okhotsk coast, Kamchatka
C. incidens — Alaska, Canada, northern states of USA
C. inornata — Canada, northern states of USA
 [*C. fumipennis*] — France
C. melanura — northern states of USA
Allotheobaldia longiareolata — France, Central Asia

IIa. Polycyclic with hibernation of the males and females:

- Culiseta annulata annulata* — England, Belgium

III. Monocyclic with larval diapause:

- **Culiseta litorea* — England, Mediterranean
 **C. setivalva* — Crimea
C. fumipennis — England, Crimea
C. morsitans morsitans — Europe, Crimea, Caucasus
C. morsitans dyari — Alaska, Canada, USA

IV. Polycyclic with larval diapause:

- **Culiseta silvestris ochroptera* — Estonia, Federal Republic of Germany
 **C. silvestris amurensis* — Amur region
C. victoriensis — Australia
C. hilli — Australia
Austrotheobaldia littleri — Australia
 [*C. annulata annulata*] — Mediterranean
 [*C. annulata subochrea*] — Central Asia
 [*C. incidens*] — southern states of the USA
C. morsitans dyari — USA (Alaska), Canada
 [*C. melanura*] — USA (Rhode Island)

V. Monocyclic with egg diapause:

- [*Culiseta victoriensis*] — Australia
 [*C. hilli*] — Australia
 [*Austrotheobaldia littleri*] — Australia

VI. Polycyclic with egg diapause:

- [*Culiseta morsitans morsitans*] — Federal Republic of Germany
 [Allotheobaldia longiareolata] — Mediterranean

VII. Polycyclic, possibly all of the stages diapausing:

- [*Culiseta annulata annulata*] — England, France, Federal Republic of Germany, German Democratic Republic, Caucasus
 [*C. melanura*] — USA (New Jersey)
 [Allotheobaldia longiareolata] — Caucasus, Syria, North Africa

VIII. Polycyclic without diapause:

- **Culiseta inconspicua* — Australia
 **C. frenchi* — Australia
C. annulata annulata — southern Europe, Syria, Lebanon
C. annulata subochrea — Central Asia, Asia Minor
C. inornata — southern states of the USA, Mexico
C. melanura — southern states of the USA
 Allotheobaldia longiareolata — Palestine, southern France

IX. Tree hole mosquitoes:

- **Theomyia fraseri* — equatorial Africa

94 We again stress that the classification of a given mosquito with some type of life form should not be regarded as permanent for that species of mosquito under all conditions and in all geographic regions, as demonstrated in a special analysis from data available in literature and the author's own material (Maslov, 1961b, 1963).

Imaginal activity: Sexual activity in the different groups of family Culicidae becomes apparent at different periods after emergence. Owen (1942) noted that the males of *Culiseta inornata* are capable of mating within 24 hr of emergence while the females can do so even within a few minutes. In most cases, mating among *Culiseta* occurs during continuous swarming: the males and females enact their bridal dance over a fairly wide area. Furthermore, there is usually a noticeable preponderance of males. Such swarms have been described by Hubert (1953) for *C. incidens*, by V.M. Popov (1950) for *C. silvestris silvestris** in Tomsk region and in special detail by Hayes (1958) for *C. melanura*. Swarming occurs for one or two hours at dusk (Hayes, Hubert and Popov). Darkness puts a stop to mosquito activity as does rain, wind and other unfavorable climatic conditions. Hayes (1958) stated that swarms of *C. melanura* fly usually at

*V.M. Popov (1950) called this mosquito *Culiseta ochroptera*.

95 heights of 3–6 m above the ground (from 1.2 to 10 m); the swarm can be frightened by a shout or a whistle, but later the mosquitoes return to the former site. These and similar observations of the behavior of different Culicidae suggest the significant role of sonic stimuli in individual and specific life periods of mosquitoes. They probably play a decisive role in the formation of the swarms of a single species and in the selection of females by the males and vice versa.

The main subjects of attack by most Culisetina mosquitoes are wild mammals and birds (Table 8); this is the reason for the limited epidemiological importance of Culisetina in regions where the vector role of these mosquitoes has been established. Within the USSR, blood-sucking by *Culiseta alaskaensis alaskaensis*, *C. annulata annulata* and *Allotheobaldia longiareolata*, has been reported on man.

The following attack man more rarely: *Culiseta bergrothi*, *C. alaskaensis indica*, *C. annulata subochrea*, *C. morsitans morsitans*, *C. silvestris amurensis* and *C. setivalva*. Reports on this subject are not available for *C. silvestris silvestris* and *C. glaphyroptera*.

The daily rhythm of the blood-sucking activity of Culisetina mosquitoes is determined, as in other species of blood-sucking Culicidae, primarily by conditions of light intensity if such unfavorable influences as the wind are strong or even incessant rain remain the same (Maslov, 1960b, 1963). During much of the feeding period, the temperature factor plays a secondary role. However, temperature acquires decisive importance in early spring and autumn when light is inadequate. Access to the objects of attack not only in a given period, but in the preceding period vitally affects the degree of aggressiveness of the mosquitoes (Haufe, 1954; Maslov, 1960b; Monchadskii, 1949, 1950, 1955). Mosquitoes under prolonged starvation, with no access to food, attack indiscriminately and attempt to surmount any impediment. If, however, in the preceding period, the population enjoyed an abundance of food, the extent of aggressiveness is very low. This phenomenon is important in the practical application of repellents, especially in investigations to evaluate the efficiency of new preparations of repellents.

In their search for food, mosquitoes can travel long distances. The investigations of Clarke (1943) on *Culiseta inornata* established a flight distance of over 20 km (14 miles) from the point of breeding. Except for Hayes' reference (1958) to the flights of *C. melanura* swarms to a height of 10 m, the limits of vertical flight of *Culiseta* mosquitoes are not known. According to Burbutis and Jobbins (1958), in New Jersey, *C. melanura* mosquitoes flew into a collec-

Table 8. Subjects attacked by Culisetina mosquitoes

Species of mosquitoes		Man	Mammals		Birds
			Large	Small	
Genus <i>Culiseta</i> , subgenus <i>Culiseta</i> s. str.					
1.	<i>C. alaskaensis alaskaensis</i>	4	4	2	2
	<i>C. alaskaensis indica</i>	1	4	-	-
2.	<i>C. annulata annulata</i>	4	4	2	2
	<i>C. annulata subochrea</i>	2	4	-	-
3.	<i>C. atlantica</i>	-	-	-	-
4.	<i>C. bergrothi</i>	2	4	-	-
5.	<i>C. glaphyoptera</i>	0	+	+	+
6.	<i>C. impatiens</i>	2	4	2	2
7.	<i>C. incidens</i>	3	4	3	3
8.	<i>C. inornata</i>	4	4	-	-
9.	<i>C. kanayamensis</i>	+	+	-	-
10.	<i>C. niveitaeniata</i>	-	-	-	-
11.	<i>C. particeps</i>	0	+	-	-
Genus <i>Culiseta</i> , subgenus <i>Culicella</i>					
12.	<i>C. atra</i>	-	-	-	-
13.	<i>C. fumipennis</i>	1	+	+	+
14.	<i>C. inconspicua</i>	1	+	+	-
15.	<i>C. litorea</i>	0	+	+	-
16.	<i>C. morsitans morsitans</i>	2	+	+	5
	<i>C. morsitans dyari</i>	1	+	+	5
17.	<i>C. nipponica</i>	-	-	-	-
18.	<i>C. setivalva</i>	+	+	-	-
19.	<i>C. silvestris amurensis</i>	1	+	+	4
	<i>C. silvestris minnesotae</i>	-	-	-	-
	<i>C. silvestris ochroptera</i>	0	+	+	+
	<i>C. silvestris silvestris</i>	0	+	+	+
Genus <i>Culiseta</i> , subgenus <i>Climacura</i>					
20.	<i>C. antipoda</i>	-	-	-	-
21.	<i>C. melanura</i>	2	+	+	5
22.	<i>C. tonnoiri</i>	+	-	-	-
Genus <i>Culiseta</i> , subgenus <i>Neotheobaldia</i>					
23.	<i>C. drummondi</i>	+	-	-	-
24.	<i>C. frenchi frenchi</i>	2	+	+	-
	<i>C. frenchi atritarsalis</i>	-	-	-	-
25.	<i>C. hilli</i>	2	+	+	-
26.	<i>C. otwayensis</i>	-	-	-	-
27.	<i>C. sylvanensis</i>	+	-	-	-
28.	<i>C. victoriensis</i>	2	+	+	-
29.	<i>C. weindorferi</i>	-	-	-	-

Genus <i>Austrotheobaldia</i>				
<i>A. littleri</i>	0	+	-	+
Genus <i>Theomyia</i>				
<i>Th. fraseri</i>	3	+	+	+
Genus <i>Allotheobaldia</i>				
<i>All. longiareolata</i>	2	+	+	4

Note: 0—does not attack; 1—attacked very rarely; 2—attacks rarely; 3—attacks rather frequently; 4—attacks often; 5—attacks very often, minus—no information, and plus—attacks recorded, but without detailed information.

tor's net close to chicken traps on the ground or at a very low height. Traps at heights of 100–120 cm or more were almost invariably deserted. Burgess and Haufe (1960) gave totally different values for *C. inornata* and *C. morsitans*: the former species (in areas devoid of forests) was found at heights of 1.5 and 7.5 m and *C. m. dyari* at heights of 1.5, 7.5 and even 15.0 m.

There are few data on the gonotrophic nature of *Culisetina* mosquitoes. In an overwhelming majority of cases a blood feed is absolutely essential for the fertilized females while autogenous egg development has been studied for only a few forms. Some references are available (Chao, 1958; Spielman, 1957*) for *C. annulata subochrea*, *C. inornata* and *Allotheobaldia longiareolata*. Rioux (1958) referred to the autogenous development of eggs as typical of Mediterranean *C. subochrea*, unlike *C. annulata*. Marshall and Staley (1936) noticed this feature even in the British *C. subochrea*. The investigations of de Boissezon (1930 and others) on *C. annulata* in Toulouse established a relation between the growth of eggs after a blood feed and environmental temperature conditions. It was found that egg growth did not occur at all in this species at temperatures under +14°C while, at 16 to 18°C, the duration of egg laying after a blood feed was 17 days and rose to 19 days at 14°C. A single female laid 100–112–150 eggs on successive occasions. Roubaud (1952), while experimenting with this same species, demonstrated the presence of a specific although unstable diapause state in hibernating females. According to his data, in the November females, the duration of the gonotrophic cycle exceeded two months at +18°C, while the females of the spring generation under the very same conditions needed only 11–16–20 days.

*The reference by Spielman (1957) concerns autogenous egg development in *Culex pipiens*, not *Culiseta* [Editor].

According to Frohne (1954a), the duration of the gonotrophic cycle in hibernating females of *C. alaskaensis* in Alaska varied from 10 to 54 days (mean = 32.2 ± 1.5 , $n = 53$); the growth of eggs in *C. impatiens* in Alaska (Frohne, 1953) was more rapid, 14.5 days (from 10 to 35); the gonotrophic cycle of *C. ornata* was only 5.3 (5–9) days (Frohne, 1953; Owen, 1942). The number of eggs laid by female *Culisetina* mosquitoes is shown in Table 3. Newkirk's work (1955) is interesting in that it indicates that in the same gonotrophic cycle, the female *C. inornata* lays the entire mass of eggs not in one, but in two clusters. According to Owen's data (1942), during a relatively long life cycle (mean 95.8 days) 14 females of *C. inornata* had several blood meals (mean = 5.57) and correspondingly multiple ovipositions.

Data on gonotrophic rhythm and number of eggs laid are few even for members of the subgenus *Culicella*, which lay eggs not in rafts but singly*. S.B. Val'kh (1957) noted that, under laboratory conditions, at temperatures of 24–26°, *C. ochroptera* from Ukraine took two days to digest the blood. Some similar reports are available even for the Australian species (Dobrotworsky, 1954) for which, under optimum temperature conditions of +8 to +10° (there is no oviposition at such high temperatures as +20 to +22°), oviposition occurred at intervals of 16–29 days after a blood feed. Under laboratory conditions, these mosquitoes oviposit singly and often not in water but on a moist substratum (filter paper). Their growth ceases with an essential diapause which is due to continuous low temperature.

In Syr Daryan *Culiseta annulata subochrea* (Maslov, 1963, 1964c**), the possible dependence of the proper growth of the ovaries and the independence of egg development on the fat production in the female has been experimentally established. For *Allotheobaldia* 97 *longiareolata* mosquitoes in the same region, a complete gonotrophic harmony has been identified. In Syr Daryan *C. alaskaensis indica* and the Far Eastern *C. bergrothi*, total maturity of the ovaries is possible only when the degree of fat production in the female is not less than 1.0***.

A specific preference of the females for ovipositing in β -mesosaprobic reservoir conditions has been noticed in four species

*Only the Australian species *Culiseta inconspicua* does not oviposit singly, but in rafts (Dobrotworsky, 1954).

**Maslov (1964c) is not cited in the References [Editor].

***Female fat production is determined by weighing the fully fed form and finding the difference in the proportion of the blood sucked to the original weight of the starved female.

studied by the author (*C. bergrothi*, *C. alaskaensis indica*, *C. annulata subochrea* and *Allotheobaldia longiareolata*) (Maslov, 1963, 1964c) and in *C. alaskaensis alaskaensis* (Frohne, 1954a) and *C. impatiens* (Frohne, 1953). As demonstrated in the example of Khabarov and Amgun *C. bergrothi*, female behavior during oviposition suggests an active selection of more favorable conditions by means of chemoreceptor structures attached to her proboscis and legs (Maslov, 1963, 1964c); this is known in the other mosquitoes of the family Culicidae (Bar-Zeev, 1960a; Ivanova, 1960; Matuo, 1957; Snodgrass, 1959; Wallis, 1954b).

GEOGRAPHIC DISTRIBUTION OF CULISETINA MOSQUITOES

Culiseta alaskaensis (Fig. 60), found in the Arctic and boreal regions of the Palaearctic and Nearctic zones, is the most widely distributed of all the species of Culisetina. In the Rocky Mountain region, *C. a. alaskaensis* is found in Mexico (Colorado and Arizona)*. In eastern Europe, it is reported from Rumania, Czechoslovakia and Yugoslavia and from the Moldavian Soviet Socialist Republic. It is known from northern Europe, almost everywhere in Siberia and is found everywhere in eastern Asia to the upper and lower Amur regions inclusive; it is very rare in central Amur and is seen only in its westernmost and northernmost regions. In the Amur valley, the eastern boundary of its distribution almost coincides with that of *Anopheles maculipennis*, that is, neither of these mosquitoes is encountered east of Zeya-Bureya watershed (Beklemishev and Zhelokhovtsev, 1945; Maslov, 1960)**. Attempts to provide an ecological interpretation of this phenomenon (Monchadskii, 1949, 1950) have not explained the factors limiting the spread of these species in the central Amur region in the east and southeast. *C. a. alaskaensis* is known from Inner Mongolia, which represents the southernmost region of the occurrence of this species in eastern Asia. In the north, it is found in the severe conditions of Taimyr Tundra. In Central Asia, the subspecies *C. a. indica* is found everywhere, distributed south to Iraq, northern India and Pakistan.

The distribution of the other members of the subgenus *Culiseta*

*This distribution is not correct as the species is not found in Mexico or Arizona [Editor].

***C. alaskaensis alaskaensis* is, however, known in the northeastern regions of central and lower Amur.

s. str. is far more restricted; they are found only in Europe and in Asia or in America. The European species *C. annulata* is an exception: it is distributed (Fig. 63) everywhere in western and eastern Europe except the Arctic zone, everywhere in the Mediterranean region except the African desert regions of Libya and Egypt, everywhere in northern Asia and Asia Minor and in the Russian Central Asian Republics, in the southern regions of European USSR, in Crimea and in the Caucasus. Furthermore, almost everywhere both subspecies have been found with each other: *C. a. annulata* and *C. a. subochrea*: the former enjoys predominant distribution in Europe and North Africa (it is a unique subspecies, found in the Caucasus and in European USSR) and the latter in the Asian regions.

- 98 Hughes (1961) studied the dispersal of mosquitoes over a 30-year period using aircraft with a fitted trap. He once detected a dead female *C. annulata* among other mosquitoes in mainland USA. The species close to *C. annulata*, that is, *C. atlantica* and *C. particeps* (Fig. 63), were distributed as follows: the former in the Azores and the latter in Central America, Cuba, Mexico and the southwestern (Nevada, Utah and Arizona) and Pacific coast (California and Oregon) states.

The range of *C. bergrothi* (Fig. 65) was confined to the northern regions of Europe (Scandinavia, Finland, the Arctic zone and northern and partly western European USSR) and, in the east, along western and eastern Siberia to the Pacific Ocean. In the Asian part of the Arctic zone it is known only in the Far Eastern Asian regions: Cape Schmidt and farther to the Bering Straits. Bozhenko (1948) reported *C. bergrothi* from eastern Kazakhstan. It is possible that a more detailed study of mosquito fauna in the southern regions of western Siberia, northern Urals and northern Kazakhstan will show that the specific range of *C. bergrothi* extends beyond these regions and possibly even to the central region of European USSR.

The last of the European species of the subgenus *Culiseta*, the southern European species *C. glaphyoptera* (Fig. 65), has been found in Austria, Federal Republic of Germany, German Democratic Republic and other countries of Central Europe, in the southern regions of eastern Europe, in the Apennines and southern Balkans, in northern Asia and in the USSR in the central Volga region and western Ukraine. The old references to its distribution in the northern regions of Europe, including the northern sections of the USSR, should be regarded as pertaining to *C. bergrothi* which is almost indistinguishable from *C. glaphyoptera* in the morphological structures of the female.

Three American species of the subgenus *Culiseta* are widely distributed. *C. impatiens* (Fig. 65) is found everywhere in the Arctic zone of the Nearctic, in Canada, in Labrador and in the Pacific Ocean coastal states to Mexico, in the southwestern, northern (except North and South Dakota) and northeastern states. There are some references from Illinois. *C. incidens* (Fig. 69) may be called a mosquito of the northwest and west. It is known to occur in the Arctic zone and Canada east to Hudson Bay, but is not found in Ontario and Labrador. Within the USA, its range is confined to the states of the Pacific Ocean coast, southwestern states, many northern and western states (Idaho, Montana, Wyoming, North Dakota, Nebraska and Michigan) and south to Oklahoma and Texas. On the contrary, the mosquito *C. inornata* (Fig. 69) is a relatively more southern form. It is found everywhere in the USA and in Canada except its northeastern territory, a major portion of Yukon, Quebec and Labrador and New Brunswick and the adjoining islands. It is not found in Alaska, but is known from Mexico and Cuba and recently this mosquito was reported from the Hawaiian Islands by means of research with aircraft (Hughes, 1961)*.

The last two species of the subgenus *Culiseta* are the Asian species *C. kanayamensis* (Fig. 65), found only in Korea and Japan, and *C. niveitaeniata* (Fig. 65), a species of the Orient known from northern India, Pakistan, Tibet, southern and partly central and northeastern China.

An analysis of the range of all species of the subgenus *Culiseta* would show that this subgenus should be described as Holarctic. Some individuals penetrate the adjoining southern regions: *C. alaskaensis indica* and *C. niveitaeniata* into the Oriental region and *C. particeps* into the Neotropical region.

- 99 Among the members of the subgenus *Culicella*, *C. morsitans*, a European and American species, is most extensively distributed. In the countries of the Old World, it has been found everywhere in Europe including European USSR, except the White Sea coast and its congruent northern sections (Fig. 75). In the east, through the central Ural region, it extends to the central and southern regions of western Siberia and northern sections of Central Asia. It is often found in the Caucasus and in Crimea, but not in the southern Ural and northern Caspian regions. Outside the European countries of the Mediterranean zone, it is known from Algeria, Asia Minor and

*See footnote concerning Hawaiian records in systematic treatment of this species on p. 196 [Editor].

Palestine. The American form of this species, *C. m. dyari* (Fig. 75), is found everywhere in the Nearctic polar regions, Canada, Labrador and the adjoining islands, in the northern and western region (Pacific Ocean coast), northeastern and eastern states and in Illinois, Indiana, Kentucky, Ohio and Colorado. As demonstrated by Barr (1957, 1959) and Price (1958), many references ascribed to this species from Minnesota and some other states in fact referred to another species, *C. silvestris minnesotae*. Possibly the distribution of *C. m. dyari* would be limited to only the more northern regions if a more detailed study were made of the fauna and ecology of mosquitoes in such states as Colorado and Kentucky.

C. fumipennis and *C. litorea* represent specific European species of the subgenus *Culicella*. The former (Fig. 69) is known everywhere in Europe, but is not found in European USSR; it has been reported from the Leningrad region, Estonia and Belorussia, the Ukraine, the Caucasus, central Ural and the southwestern portions of western Siberia. Outside the European part of the Mediterranean region, it is known from Algeria and Asia Minor. *C. litorea* (Fig. 75) has a narrower range and is known from Great Britain and the westernmost parts of western Europe and the Mediterranean region; it has also been seen from Czechoslovakia, Algeria and the Mediterranean islands.

The distribution of *C. setivalva* (Fig. 69), which has been found only in Crimea (southern coast) and in Anatolia, has an even more limited range. A scattered range is typical of *Culiseta silvestris* (Fig. 82); its western form, *C. s. ochroptera*, is found in the German Democratic Republic, Federal Republic of Germany, Czechoslovakia and in some northern and western regions of European USSR. Another subspecies, *C. s. silvestris*, is known in the central and southern regions of European USSR (this has also been described as a new species around Moscow) and from the central Ural and southern sections of western Siberia. The third subspecies, *C. s. amurensis*, is distributed in eastern Asia: central and in part lower Amur, Primorye and northeastern China (Heilungkiang Province). The fourth subspecies, *C. s. minnesotae*, has been reported from North America (Minnesota, New York, New Jersey, Delaware and Wisconsin). The East Asian species with an extremely narrow range, *C. nipponica*, (Fig. 69) is confined to only some zones of Japan and Korea. Two species of the subgenus *Culicella* have been found in the Australian regions, *C. atra* only in western Australia (Fig. 75) and *C. inconspicua* in Victoria, New South Wales and Tasmania (Fig. 75).

As the above data indicate, the subgenus *Culicella* on the whole

may be called a subgenus of the southern Holarctic and partly of Notogaea.

Of the three members of the subgenus *Climacura**, *C. melanura* is distributed mostly in the southeastern states of the USA (Fig. 87) and north to Iowa, Wisconsin, Michigan and Nebraska and west to Colorado, Oklahoma and Texas. Outside the Nearctic region, it has not been reported in the south except by Ortiz (1960) for northern Mexico. The second species of this subgenus, *C. antipodea*, described very recently (Dobrotworsky, 1962), is known from Queensland and Victoria (Fig. 87). The third species of the subgenus *Climacura*, *C. tonnoiri*, is an inhabitant of New Zealand (Fig. 87).

The subgenus *Neotheobaldia* includes seven Australian species, six of which are known only from Victoria: *C. drummondi*, *C. frenchi*, *C. hilli*, *C. otwayensis*, *C. sylvanensis* and *C. victoriensis* (Fig. 82) and the seventh species, *C. weindorferi*, has been reported from Tasmania (Fig. 82).

The Australian monotypic genus, *Austrotheobaldia*, with a lone representative, *A. littleri*, is distributed in Victoria, New South Wales and Tasmania (Fig. 87). Another monotypic genus, *Theomyia*, with a single species *Th. fraseri*, is known from equatorial Africa (Fig. 87) and is found in Kenya, Uganda, Sierra Leone, Congo, Nigeria and Cameroons.

The monotypic genus *Allotheobaldia* with the species *A. longiareolata* (Fig. 87) is extensively distributed in the Mediterranean region and is found in some regions of central and eastern Europe and reported even in Britain. In European USSR, it is known from southwestern and central Ukraine, from Donbass and from southern Ural. Outside the Mediterranean zone in the east, it is widely distributed in the western deserts and Central Asia, to the southernmost regions of western Siberia in the north. In Africa, it is known from the Sahara, Eritrea, Somali and Sudan; it is absent near the equator but found again in South Africa including Transvaal. In southwest Asia, it is found up to the Orient and is reported from northern India and Pakistan.

The subtribe Culisetina has a worldwide geographic distribu-

*Two additional species have been described: *C. novaezealandiae* Pillai from New Zealand (Pillai, J.S. 1966. *Culiseta novaezealandiae*, a new species of the subgenus *Climacura* Felt (Diptera: Culicidae: Culicini), with notes on its ecology and development. Trans. R. Soc. N.Z., Zool. 8: 125-133) and *C. marchettei* from Malaysia (Garcia, R., J. Jeffrey and A. Rudnick, 1969. *Culiseta marchettei*, a new species of the subgenus *Climacura* Howard, Dyar and Knab, with notes on its biology (Diptera: Culicidae). J. Med. Entomol. 6: 251-256) [Editor].

tion. The mosquitoes of this group are not found only in South America and in Southeast Asia, including the Malay Archipelago*.

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*The discovery of *C. marchettei* in Malaysia changes this distribution [Editor].

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*Erroneous citation. This species was described in Becker, Th. 1908. Dipteren der Kanarischen Inseln. *Mitt. Zool. Mus. Berl.*, 4(1): 1-180 [Editor].

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SYSTEMATICS

SOME GENERAL ASPECTS OF SYSTEMATICS

Speciation phylogeny is the evolutionary process representing the successive stage of ontogenesis. Although phylogeny and ontogeny represent a common process, they are not identical. Some new, biologically useful characteristics evolve with every new generation through the process of natural selection. Some older features, which are biologically useful, are preserved and become increasingly stabilized. Other features, which are not biologically useful, are preserved or reduced with an insignificant role in the evolutionary process. Adverse biological features constitute the bulk of the reduced features. The concentration of useful new qualities and the vigorous shedding of deleterious and antiquated ones (each time in its typical way under different conditions) in a specific sequence of natural selection is a steady and continuous process and, at the same time, a shift or interruption in the continuous growth of a species. In some rare instances, the evolution of a new species occurs rapidly within the course of a few hundred generations, but such instances in the natural environment are not a rule, but a rare exception. Speciation is a gradual and very slow process, at least in the case of insects.

Intraspecific variability and the stage of speciation may be represented in the form of the following higher categories:

a) *Variations*: These are individual phenotypic deviations which result from the responses of growing individuals to changes in the external or internal environment. These could be individually significant, have adaptive importance or be quite unimportant in the growth of any individual specimen. The variations could be manifested in morphological structures or in the characteristics of growth, physiology, ecology, ethology, and so on.

b) *Morphs*: These are specific variations in morphology which represent monotypic, systematic responses of the specimens to certain influences (seasonal, thermal or light, chemical, nutritional and others).

c) *Populations*: These are local concentrations of specimens of a given species including the diverse variations and morphs found in

that region. The local populations of a given species are not identical in the various topographic-geographic zones and are represented by the common variations in a given zones; that is, among polymorphic species, the populations reflect a specific local evolutionary tendency.

- 113 d) *Subspecies*: Unlike the variations and morphs, subspecies are characterized by relative stabilization of morphological, physiological and other features due to selective and regular environmental factors prevailing in a given section of the species range (geographical subspecies) or in a given group of biotopes (ecological subspecies). Such factors vary in other sections of the range or other groups of biotopes. Natural hybridization is possible between specimens of sympatric subspecies but, as conditions change, the subspecies become capable of transforming quickly one into another.

e) *Species*: This is the supraindividual grouping at the evolutionary level represented by a group of dissimilar individuals, genetically irreversibly separated from the other such groups, mostly in their morphological, physiological, ecological, ethological and other features and protected from crossing by virtue of physiology, space or season.

For practical systematics, only the latter two, species and subspecies, from among these higher categories, which reflect the evolutionary process, can be regarded as essential and adequate as taxa. In determining the taxonomic importance of the various factors, it would be best to identify and establish those qualities of each species which determine the course of individual growth and the accumulation of proteins and other body substances of the living body and are specific for a given species. Attempts to find biochemical and cytogenetic approaches to taxonomy are therefore wholly justified. However, achievements to date have had little practical application and hence, while applying the accessible characteristics of taxonomic importance (morphological, physiological, ecological, geographical, ethological, and others) in practical taxonomy, for many reasons special attention should be given in the first instance to structural characteristics.

Taxonomists rarely find characteristics which show distinct differentiation of proximate species and subspecies. Usually they must rely on overlapping characteristics. We find it difficult to justify the concept of "type" maintained in new descriptions of some taxa. The type does not reflect intraspecific differences and with an abundance of synonyms tends to confuse taxonomists. It is therefore essential to develop and propagate the concept of "population".

The accuracy, applicability and justification of the quantitative approach with extensive use of biometric criteria (criteria of reliability, coefficients of differences, coefficients of discrimination, and others) have been demonstrated in an analysis and taxonomic revision of *Culisetina* mosquitoes (Maslov, 1963, 1964a). At the same time we have emphasized that specific biological features must be considered while resorting to mathematical interpretations. Consequently, when using biometric criteria, the actual characteristics of the populations, subspecies and species under comparison should always be considered.

Although the name of the genus *Theobaldia* (Neveu-Lemaire, 1902) was established earlier than *Culiseta* (Felt, 1904), the name *Theobaldia* should be discarded for homonymic reasons according to the rules of zoological nomenclature since it was already assigned to a mollusk* genus; mosquitoes belonging to this genus should be called *Culiseta* (Maslov, 1963, 1964a).

A comparison of the morphological structures in all growth phases of the mosquitoes *Allotheobaldia longiareolata*, *Theomyia fraseri* and *Austrotheobaldia littleri* with all members of *Culiseta* showed (Maslov, 1963, 1964a) that the grouping of these species into a common genus with the true *Culiseta* was based on a few features found in the other Culicidae also. An overwhelming number of morphological features of these species, however, sharply differentiate them from *Culiseta*. It is thus possible to raise the above three mosquitoes from the subgeneric ranks to the levels of genera and group them with true *Culiseta* in a common subtribe, *Culisetina* Masl. (Maslov, 1964a).

The author has revised (Maslov, 1963, 1964a)** the specific and subspecific groupings and established the following status of mosquitoes, formerly in the genus *Theobaldia*:

*Subgenus *Theobaldinus* nov., Nevill, 1878, pp. 275-277; *Theobaldia* Nevill (instead of *Theobaldinus*), Fischer, 1885, p. 744.

**The description of the larvae of *Theobaldia indica* Edw. given by Qutubuddin (1952) and his inclusion of this species in the subgenus *Allotheobaldia* are erroneous. The author (Maslov) has larvae (and adult mosquitoes) of *Culiseta alaskaensis indica* from India (Punjab) which were given to him by Barraud. A careful study of these specimens does not confirm the findings of Qutubuddin. Probably, Qutubuddin's description of larvae of *Theobaldia indica* pertained to some aberrant specimens of *Allotheobaldia longiareolata*.

Family Culicidae

Subfamily Culicinae

Tribe Culisetini (Stone, 1956: 333)

Subtribe Culisetina (Maslov, 1964a: 198)

Genus *Culiseta* (Felt, 1904: 319c) with the subgenera*Culiseta* (Felt, 1904: 391c)*Culicella* (Felt, 1904: 391c)*Climacura* (Howard, Dyar and Knab, 1915: 452)*Neotheobaldia* (Dobrotworsky, 1954: 68)Genus *Austrotheobaldia* (Dobrotworsky, 1954: 68, comb. nov.)Genus *Theomyia* (Edwards, 1930: 303, comb. nov.)Genus *Allotheobaldia* (Brolemann, 1919: 90, comb. nov.)

The origin and the evolutionary course of mosquitoes have not been thoroughly studied. However, among Culisetina, we find some primitive features in the larval and imaginal structures and ecological and ethological (at least larval) characteristics which have been seen before and which could explain the possible phylogenetic relations of Culisetina mosquitoes with other, more specialized, groups (see particularly: Monchadskii, 1937 and Rodendorf, 1964). Conclusions on the centers of origin and courses of evolution of different groups in the animal kingdom are possible only when abundant data describing the contemporary position of each group (comparative morphology, comparative physiology, ecology, ethology, geographical distribution, and so on) are available. Such information on Culicidae mosquitoes is far from adequate. In addition, more conclusive palaeontological data is needed; they are very few for mosquitoes in general and totally absent for Culisetina. Consequently, a discussion of the origin and evolution of these mosquitoes, including the ancient region of their origin and distribution, is presently possible only on the basis of indirect evidence and that too only tentatively, for example, in other works concerning the origin and evolution of blood-sucking mosquitoes, especially the works of Monchadskii (1937) and Edwards (1926a).

The most primitive of the subgenera, *Culiseta* s. str., is represented by Boreal-Holarctic species and among them the most primitive species in all respects are *C. impatiens*, *C. alaskaensis* and especially *C. bergrothi*. All of them range up to the high horizons of the trans-Polar region. On the other hand, the more specialized species, especially the subgenus *Culicella*, does not extend far north.

Two subgenera (*Climacura* and *Neotheobaldia*) and the three newly isolated monotypic genera have no representatives in the areas of severe climatic conditions.

This suggests the north as the primary center of origin of the most primitive Culisetina and, in the opinion of the author, such a center could have been in northeastern Asia and northwestern America (Bering Sea zone). From there, the old "*Protoculisetina*" spread southwest and southeast. Objections to this view are based primarily on the fact that species with life form V, monocyclic species with egg diapause, characteristic of the north, are not found among Culisetina mosquitoes, including the subgenus *Culiseta* s. str. of genus *Culiseta*. The opponents of the theory of northern origin of *Culiseta* have offered an impressive argument suggesting that mosquitoes with life forms I, III and so on could have originated only in mild or moderate climate conditions, but not under severe Arctic conditions. This is, of course, justifiable. But we can also justify the origin of mosquitoes of the family Culicidae at least in the Early Cretaceous period of the Mesozoic, if not the Jurassic (Rodendorf, 1946, 1964; Edwards, 1926b, 1932a)*. Even Culisetina mosquitoes are not an exception here and we know that at the end of the Mesozoic and Tertiary periods the climate of northeastern Asia was not very severe. It is therefore not surprising that the Bering-trans-Polar zone, which today has severe climatic conditions, enjoyed such a mild climate in the Late Mesozoic or Early Tertiary that magnolias, palms and other
 116 subtropical vegetation were present. Species with life forms adapted to temperate or even warm climatic conditions could have evolved there. During subsequent cooling, some species or groups of species adapted themselves to these new conditions, while preserving the typical features of their origin in a region with a moderately warm climate. Such examples are plentiful in the Far East not only among the different orders of the insect class, but among other types of the animal kingdom.

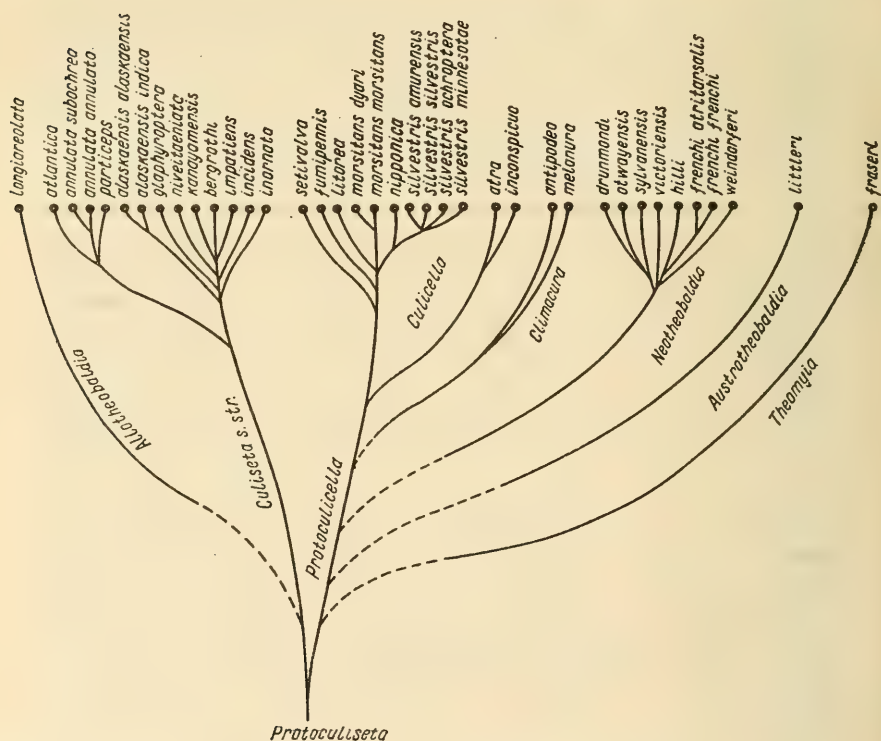
Subgenus *Culicella* probably originated in the lower latitudes of Europe. From there these mosquitoes could have penetrated into the Nearctic through the Atlantic link and into the Notogaea through the Eurasian link. Possibly a more detailed faunistic study in Southeast Asia and in the islands of the Malay Archipelago will fill the gaps in our knowledge of the distribution of the subgenus *Culicella*.**

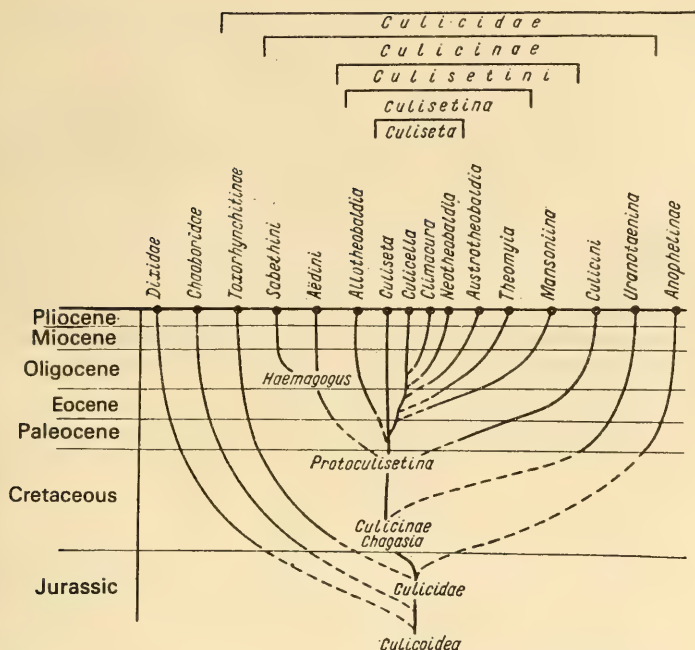
*Reliable palaeontological data for the contemporary genera of Culicidae family are available only from Tertiary rocks (Rodendorf, 1964).

**See prior footnote on p. 127 concerning *C. marchettei* [Editor].

Probably as a result of further evolution in the group of the older *Culicella* (Fig. 57), *Neotheobaldia* and *Austrotheobaldia* penetrated Australia as did *Climacura* in America and *Notogaea* and *Theomyia* in equatorial Africa. The origin of *Allotheobaldia* is very vague: possibly this monotypic genus is directly related to *Culiseta* s. str. (Fig. 57), having separated from some of its ancient Mediterranean representatives.

The genetic relations of *Ficalbia* mosquitoes and later of *Mansonia* with members of the subgenus *Culicella* have often been noticed (Hopkins, 1952; Monchadskii, 1937). It is possible that the very extreme adaptation to plankton feeding was responsible (from the ancient "*Protoculicella*") for the evolution of Culicini, while adaptation to scraping and periphyton feeding (through "*Protoculiseta*") to the evolution of Aedini and Sabethini (Fig. 58).





116 Fig. 58. Scheme showing phylogenetic relations within the family Culicidae. (Time period from top to bottom, Pliocene-Miocene-Oligocene-Eocene-Paleocene-Cretaceous-Jurassic).

IDENTIFICATION KEY FOR MOSQUITOES*

A. Females

- 1 (64). Radial setae** present (Fig. 19).
- 2 (63). Punctate pattern of large spots represented by accumulations of broad white scales absent on the femora and tibiae. Eighth sternite of usual form without prominent lobes and deep pits between them (Fig. 25).

*While differing sharply in the morphological characteristics of larvae, the species of different subgenera are often very close to each other in imaginal structures. Hence in the identification key for females, the differential-diagnostic characters are not recognized for the subgenera *Climacura* H.D.K. (Howard, Dyar and Knab) and *Neotheobaldia* Dobrotw. The same is true for the males of the subgenera *Culiseta* Felt, *Culicella* Felt and *Climacura* H.D.K.

**This also pertains to the setae situated ventrally at the base of the subcosta [Editor].

- 3 (62). Postspiracular scales absent 1. Genus **Culiseta** Felt.
- 4 (37). Spiracular setae well developed, not less than 4-5 in number (Fig. 13).
- 5 (26). Crossveins as a rule merge with one another (Fig. 20, c, 1); if, however, they are separated, it is by less than the length of m-cu (index less than 1.0) . . subgenus **Culiseta** s. str.
- 6 (15). Tarsi with fairly broad basla rings.
- 7 (8). On the wing veins Rs and M (proximal to crossveins) and on the forks R₂, R₃, R₁ and R₂, there are concentrations of scales in the form of bands (Fig. 68, a); the length of which exceeds twice their width. Extremely narrow basal ring on the tarsi. 7. **C. (s. str.) incidens** Thoms.
- 8 (7). Accumulation of scales on the wing veins in the form of ordinary spots where the veins branch (Fig. 4, 4-6). Basal tarsal rings broad: on the second and third segments of the hind-tarsi, their width is not less than twice the tarsal thickness in that region (Fig. 17, 2-4).
- 9 (14). Femora with preapical light-colored rings (Fig. 17, 4).
- 10 (11). First segment of hindtarsi with light-colored rings medially (Fig. 17, 4). Second abdominal tergite with median band of light-colored scales separate from the basal transverse band (Fig. 21, 7) 2. **C. (s. str.) annulata** Schr.
- a (b). Body color dark brown or black; contrasting pattern of dark and light-colored scales on legs and abdominal tergites . . . 2a. **C. annulata subochrea** Schr.
- b (a). Body color light brown or ocherous brown; pattern of dark and light-colored scales on legs and abdominal tergites not distinct, diffuse. 2b. **C. annulata subochrea** Edw.
- 11 (10). First segment of hindtarsi without light-colored median rings. Second abdominal tergite without median longitudinal band of light-colored scales.
- 12 (13). Abdominal tergites with distinct, complete rather narrow, basal bands of light-colored scales. Femora and tibiae anteriorly usually with a significant admixture of light-colored scales 11. **C. (s. str.) particeps** Adams.
- 118 13 (12). Abdominal tergites without basal light-colored bands, but only with tiny lateral spots of light-colored scales. Femora and tibiae without the mixture of light-colored scales, uniformly dark-colored 3. **C. (s. str.) atlantica** Edw.
- 14 (9). Femora without preapical light-colored rings (Fig. 17, 3) 1. **C. (s. str.) alaskaensis** Ludl.

- a(b). Body color dark brown or black. Pattern of dark and light-colored scales on the tarsi and abdominal tergites in contrast. Wing venation with unicolorous scales 1a. *C. alaskaensis alaskaensis* Ludl.
- b(a). Body color light brown or ocherous brown. Pattern of dark and light-colored scales on the tarsi and abdominal tergites not in contrast, diffuse. Fairly significant admixture of light-colored scales on the wing veins 1b. *C. alaskaensis indica* Edw.
- 15 (6). Light-colored rings absent on the tarsi.
- 16 (23). Wing spots—concentrations of scales—present although not always distinct (Fig. 4, 2 and 3). Palps with scattered light-colored scales or uniformly dark. Orbital margins fringed with tiny falciform scales.
- 17 (18). Scutellum covered with broad lanceolate white scales. As a rule 10 or more lower sterno-pleural setae present 10. *C. (s. str.) niveitaeniata* Theo.
- 18 (17). Scutellum covered with yellowish, narrow, falciform scales.
- 19 (20). Palp usually homogeneously dark-colored or with stray, scattered light-colored scales. Lower sterno-pleural setae usually less than 10 4. *C. (s. str.) bergrothi* Edw.
- 20 (21). Palps usually with scattered light-colored scales.
- 21 (22). Basal light-colored bands of abdominal tergites of uniform width or slightly broadened medially 6. *C. (s. str.) impatiens* Wlk.
- 22 (21). Basal light-colored bands of abdominal tergites distinctly pinched medially 9. *C. (s. str.) kanayamensis* Yam.
- 23 (16). Wing spots absent or faintly noticeable.
- 24 (25). Palps with scattered light-colored scales. Spiracular setae not more than 10–12 8. *C. (s. str.) inornata* Will.
- 25 (24). Palps homogeneously dark-colored. Spiracular setae more than 15 5. *C. (s. str.) glaphyroptera* Schiner.
- 26 (5). Crossvein m-cu closer to the wing base than R-M at least by a distance equal to the length of the m-cu itself (index over 1.0) (Fig. 20, c, 2) Subgenus *Culicella* Felt.
- 27 (32). On the abdominal sternites there is usually a pattern of dark-colored scales in the form of the letter V with the pointed end turned forward (Fig. 21, 20); if it is absent, the light-colored rings are absent or are faintly seen on the three distal tarsal segments, while the light-colored scales are especially abundant on the proboscis downward and on the flanks in the median one-third portion.

- 28 (29). Tarsal rings present in all tarsal segments in the articulations apically and basally (Fig. 17, 5) 13. **C. (Culicella) fumipennis** Steph.
- 29 (28). Rings not present in all tarsal segments.
- 30 (31). On the hindlegs, all tarsal segments with distinctly developed rings at the base of each segment. Mid- and hindfemora anteriorly usually with a distinct longitudinal band of light-colored (golden) scales 18. **C. (Culicella) setivalva** Masl.
- 31 (30). On last 2-3 tarsal segments or hindlegs rings absent or faintly seen 15. **C. (Culicella) litorea** Shute.
- 32 (27). On the abdominal sternites V-shaped pattern absent.
- 33 (36). Light-colored bands present on the abdominal tergites.
- 34 (35). Light-colored bands disposed only at the base of abdominal tergites. Wing spots absent 16. **C. (Culicella) morsitans** Theo.
- a (b). Ratio of the length of the femur to that of proboscis in all three pairs of legs usually equal to or more than one. . . 16a. **C. morsitans morsitans** Theo.
- b (a). Ratio of the length of the femur to that of the proboscis in all three pairs of legs invariably much less than one 16b. **C. morsitans dyari** Coq.
- 35 (34). Light-colored bands occupy the proximal and distal regions of tergites. A distinct spot at the base of the wing vein R_{4+5} . . 19. **C. (Culicella) silvestris** Sching. (Shing.)
- a (b). Proximal and distal light-colored tergal bands joined with each other by narrow lateral bands of the same light-colored scales. On the tarsi, the apical light-colored rings seen on the first and second segments . . . 19d. **C. silvestris silvestris** Sching. (Shing.)
- b (a). On the tergites only the basal and apical bands not joined by longitudinal bands. Eighth tergite wholly covered with light-colored scales.
- c (d). In the basal half of the costal vein, there is a perceptible admixture of light colored scales. Apical (more rarely also the basal) tergal band usually pinched and sometimes even interrupted in the middle of the tergite. On the articulations of the first-second and second-third tarsal segments, the apical-basal rings seen distinctly 19b. **C. silvestris minnesotae** Barr.

- d (c). Costal vein with uniformly dark-colored scales. Light-colored tarsal rings very weakly developed
 19c. **C. silvestris ochroptera** Reus.
- 36 (33). Abdominal tergites uniformly dark-colored or with a few scattered light-colored scales, sometimes with extremely narrow basal bands (Fig. 21, 2 and 3)
 19a. **C. silvestris amurensis** Masl.
- 37 (4). Spiracular setae weakly developed, numbering 3-5.
- 38 (39). Dorsal surface of proboscis with dark-colored and ventral surface with light-colored scales; only 2 short, thin spiracular setae 14. **C. (Culicella) inconspicua** Lee.
- 39 (38). Proboscis uniformly dark-colored. Not less than 3 spiracular setae.
- 40 (43). Anterior pronotal lobe devoid of setae and scales.
- 41 (42). Abdominal tergites covered with reddish-brown scales.
 29. **C. (Neotheobaldia) weindorferi** Edw.
- 42 (41). Abdominal sternites covered with light-colored scales or with a small admixture of dark-colored scales
 21. **C. (Climacura) melanura** Coq.
- 43 (40). On the anterior pronotal lobe are seen setae, often even scales.
- 44 (45). Abdominal sternites completely covered with black scales.
 20. **C. (Climacura) antipodea** Dobrotw.
- 45 (44). Abdominal sternites light-colored or with an admixture of dark-colored scales; if they are uniformly dark-colored, then brownish and not black scales.
- 46 (53). Tarsi of all legs uniformly dark-colored.
- 47 (50). Abdominal sternites uniformly dark-colored with brownish or purple scales.
- 120 48 (49). Sternites (and tergites) covered with dark purple scales, absent basally where, as a result, indistinct bands are formed. Only one strong lower mesoepimeral seta
 22. **C. (Climacura) tonnoiri** Edw.
- 49 (48). Abdominal sternites covered with brownish scales. Two strong lower mesoepimeral seta
 26. **C. (Neotheobaldia) otwayensis** Dobrotw.
- 50 (47). Abdominal sternites not covered with uniformly dark-colored scales.
- 51 (52). Abdominal sternites completely covered with light-colored scales. Only one strong lower mesoepimeral seta
 12. **C. (Culicella) atra** Lèe.

- 52 (51). Abdominal sternites light-colored, usually with an admixture of dark-colored scales. Two strong lower mesoepimeral setae 24b. **C. frenchi atritarsalis** Dobrotw.
- 53 (46). At least the last 2 tarsal segments entirely light-colored. Subgenus **Neotheobaldia** Dobrotw.
- 54 (57). At least two basal segments of foretarsus uniformly dark-colored.
- 55 (56). Three apical segments of all tarsi entirely light-colored. 27. **C. (Neotheobaldia) sylvanensis** Dobrotw.
- 56 (55). Two apical segments of all tarsi entirely light-colored. 25. **C. (Neotheobaldia) hilli** Edw.
- 57 (54). At least two basal segments of foretarsi with light-colored rings or spots of light-colored scales.
- 58 (61). Only basal, light-colored rings or spots of light-colored scales on the anterior 2 segments of all tarsi.
- 59 (60). Fore- and midtarsi with small spots of light-colored scales at the base of the anterior two segments; last 3 segments entirely light-colored. Only 1 strong lower mesoepimeral seta. 23. **C. (Neotheobaldia) drummondi** Dobrotw.
- 60 (59). Fore- and midtarsi with distinct light-colored basal rings on the anterior 3 segments; only the two latter segments entirely light-colored. Two or 3 strong lower mesoepimeral setae 28. **C. (Neotheobaldia) victoriensis** Dobrotw.
- 61 (58). Narrow apical light-colored rings on the 2 basal segments of fore- and midtarsi 24a. **C. (Neotheobaldia) frenchi** Theo.
- 62 (3). Postspiracular scales present 2. Genus **Austrotheobaldia** Dobrotw.
(The genus consists of a single species ... *A. littleri* Tayl.)
- 63 (2). Distinct punctate pattern of prominent light-colored spots on the femora and tibiae. Eighth sternite with 2 broad lobes and a deep groove between them (Fig. 25) 4. Genus **Allotheobaldia** Brol.
(The genus consists of a single species—*A. longiareolata* Macq.)
- 64 (1). Radial setae absent 3. Genus **Theomyia** Edw.
(The genus consists of a single species—*Th. fraseri* Edw.).

B. Males

- 1 (58). Palps relatively short or long but invariably longer than the proboscis.

- 2(45). Palps long, distinctly longer than the proboscis: if not longer than the proboscis, then spiracular setae distinctly formed and lateral lobes of gonofurca not long. Gonocoxite simple, in the form of an extended cone. Ninth tergite simple with two fairly distinct lobes (Fig. 23).
- 121 3(42). Lobes of gonofurca not long, less than one-half of the length of the gonocoxite; strong setae usually at its apex (Fig. 23) . . . Genus **Culiseta** Felt. (subgenera **Culiseta** s. str., **Culicella** Felt and **Climacura** H.D.K.).
- 4(15). Distinct preapical or apical lobes present on the median portion of gonocoxite (Figs. 59, a and 66, a).
- 5(14). On the distal margin of the 8th tergite or on its extended median lobe, heavy spines also present in addition to the usual long setae (Figs. 59, a; 64).
- 6(7). Apical bulging lobes right at the apex of gonocoxite; long lamellar branches at its tuft (Fig. 66, a). Each lobe of gonofurca with two uniformly flexed strong setae 5. **C.** (s. str.) **glaphyroptera** Schiner.
- 7(6). Apical processes located near apex of gonocoxite; it is flat or slightly bulging and without long lamellar branches.
- 8(9). Along the margin of the 8th tergite, a regular row of strong spines. Phallus weakly sclerotized. Lobes of gonofurca without strong setae (Fig. 67, a) 6. **C.** (s. str.) **impatiens** Wlk.
- 9(8). On the lobes of the 8th tergite, one or more heavy spines arranged haphazardly and not in a regular row. Lobes of gonofurca with strong setae. Phallus fairly heavily sclerotized.
- 10(11). Phallus sclerotization relatively weak. Apical process tiny, with long setae, among which one stands out prominently in length and thickness. On the 8th lobe of the tergite, a few (4–8) spines. Lobes of gonofurca with two weakly curved setae (Fig. 68, b) 7. **C.** (s. str.) **incidens** Thoms.
- 11(10). Phallus in the form of two strongly sclerotized, flattened, semiconical valves (Fig. 74, a).
- 12(13). Flat, distinct preapical lateral lobes densely covered with short setae. Lateral lobes of gonofurca with two strong setae broken sharply at an angle. On the lobes of the 8th tergite, more than two (usually over 6–7) spines. Phallic valves with apices bent sharply sideways (Fig. 59, a) 1. **C.** (s. str.) **alaskaensis** Ludl.
- a (b). Setae on the lateral lobes of gonofurca broken in their apical one-third la. **C. alaskaensis alaskaensis** Ludl.

- b(a). Setae on the lateral lobes of gonofurca broken beyond their center 1b. **C. alaskaensis indica** Edw.
- 13 (12). Long setae on a small apical process. That of gonofurca with three weakly flexed setae. Lobe of the 8th tergite with a single short, strong spine (Fig. 73, a) 11. **C. (s. str.) particeps** Adams.
- 14 (5). Distal margin of the 8th tergite without spines. On the bulging apical lobe, a tuft of long hairy appendages present. Two sharply broken setae on each of the lateral lobes of gonofurca (Fig. 72, a) ... 10. **C. (s. str.) niveitaeniata** Theo.
- 15 (4). Distinct apical lobes absent; sometimes a section with very densely set setae found in the apical zone of the gonocoxite.
- 16 (19). In the mediodistal one-third of the gonocoxite is seen a section with very densely set setae. Phallus in the form of two heavily sclerotized, flattened, semiconical valves (Fig. 74, a).
- 17 (18). Lobes of the 9th tergite with sharply projecting distal sclerotizations and short, strong spines. Lateral lobe of gonofurca without strong setae (Fig. 70, a) 8. **C. (s. str.) inornata** Will.
- 122 18 (17). Lobes of the 9th tergite of usual structure, without pointed, distal sclerotization and with relatively long setae. 2. **C. (s. str.) annulata** Schr.
- a (b). Lateral lobes of gonofurca with two (rarely three) strong setae. On the lobes of the 8th tergite, spines absent or very few (up to 4) 2a. **C. annulata annulata** Schr.
- b (a). Lateral lobes of gonofurca with three or more (very rarely 2) strong setae. On the lobes of the 8th tergite, usually more than 4 (0-8) spines 2b. **C. annulata subochrea** Edw.
- 19 (16). In the mediodistal one-third of gonocoxite, concentrations of setae absent. Phallus as a rule weakly sclerotized and usually oval-shaped like an egg.
- 20 (21). On the gonocoxite and the 8th tergite, apart from the usual setae there are heavy, long, straight nail-shaped setae or spines. The two heavy setae on the lateral lobes of gonofurca also similar (Fig. 80) ... 18. **C. (Culicella) setivalva** Masl.
- 21 (20). Setae common on the gonocoxite and the 8th tergite.
- 22 (35). Antennal index (ratio of the total length of the first four segments of antenna to the length of the proboscis) more than one.

- 23 (24). On each of the verrucae of gonofurca, invariably two thin, bent setae. The lobes of the 8th tergite with more than 10 spines (Fig. 64) 4. **C. (s. str.) bergrothi** Edw.
- 24 (23). On the lateral lobes of gonofurca, usually more than two setae. Spines present (their number not more than 10) or absent on the lobes of the 8th tergite.
- 25 (30). Spines absent on the lobes of the 8th tergite.
- 26 (27). Phallus with straight lateral surfaces and transverse, sharply projecting, heavily sclerotized, distal margin (Figs. 83, a and 84) . . . 19b. **C. (Culicella) silvestris minnesotae** Barr.
19d. **C. (Culicella) silvestris silvestris** Sching. (Shing.).
- 27 (26). Phallus oval-shaped like an egg, without strong distal sclerotization.
- 28 (29). Ratio of the length of the gonotelopod to that of gonocoxite less than 1/2. The lateral lobes of gonofurca with 2–3 strong setae . . . 20. **C. (Climacura) antipodea** Dobrotw.
- 29 (28). Ratio of the length of the gonotelopod to that of gonocoxite about 2/3. The lateral lobe of gonofurca, with 4–5 strong setae 21. **C. (Climacura) melanura** Coq.
- 30 (25). Spines present on the lobe of the 8th tergite.
- 31 (32). Distal segments of antenna (or the last one) distinctly enlarged (Fig. 9, B and C) . . 16. **C. (Culicella) morsitans** Theo.
a (b). The lobes of the 8th tergite with usually less than 8 (3–10) spines . . . 16a. **C. morsitans morsitans** Theo.
b (a). The lobes of the 8th tergite with 8 or more (8–10) spines 16b. **C. morsitans dyari** Coq.
- 32 (31). Distal segments of antenna same thickness as the proximal ones (Fig. 9, A).
- 33 (34). On each lateral lobe of the gonofurca, 3–4 heavy setae 13. **C. (Culicella) fumipennis** Steph.
- 34 (33). On each lateral lobe of gonofurca, usually more than 4 heavy setae . . . 19. **C. (Culicella) silvestris** Sching. (Shing.).
a (b). On the lobes of the 8th tergite, usually 5 spines present. The length of the anterior tibia more than that of the proboscis . . . 19a. **C. silvestris amurensis** Masl.
b (a). On each lobe of the 8th tergite, usually 6–8 spines. Anterior tibia shorter than the proboscis
. 19c. **C. silvestris ochroptera** Peus.
- 35 (22). Antennal index less than one.
- 36 (39). Strong setae present on the lateral lobe of gonofurca.
- 37 (38). Base of gonotelopod distinctly bulging. On the lobes of the 8th tergite, spines absent or very few
. 15. **C. (Culicella) litorea** Shute.

- 38 (37). Base of gonotelopod not bulging. At least 10 spines on the lobes of the 8th tergite (Fig. 71, a) 9. **C. (s. str.) kanayamensis** Yam.
- 39 (36). Apices of the lateral lobes of gonofurca covered with fine setae; strong setae absent.
- 40 (41). On each lobe of the 9th tergite, 3-4 setae present. 12. **C. (Culicella) atra** Lee.
- 41 (40). On each lobe of the 9th tergite, 7-8 setae present 14. **C. (Culicella) inconspicua** Lee.
- 42 (3). Lateral lobe of gonofurca very high, extending beyond the center (usually up to $2/3$) of the gonocoxite; its apex covered with fairly long and dense setae, without strong setae. ... Subgenus *Neotheobaldia* Dobrotw.
- 43 (44). Usually not less than 10 (9-15) setae on the lobes of the 9th tergite. Phallus enlarged distally, but without denticles (Fig. 90) 24. **C. (Neotheobaldia) frenchi** Theo.
- 44 (43). Not more than 10 (8-10) setae on the lobes of the 9th tergite. Very few small denticles on the enlarged distal margin of the phallus (Fig. 93, a) 27. **C. (Neotheobaldia) sylvanensis** Dobrotw.
- 45 (2). Antennae of equal length or slightly shorter than the proboscis.
- 46 (57). Gonocoxite simple, extended like a cone. Gonotelopod with one apical appendage. Ninth tergite simple.
- 47 (52). Palps of equal length as the proboscis, sometimes slightly longer. The apex of the lateral lobe of gonofurca descends beyond the center of the gonocoxite.
- 48 (49). Lateral lobe of gonofurca does not reach the apical one-third of the gonocoxite (index over $1/2$, not less than $2/3$). Phallus almost rectangular with flat, weakly sclerotized apex (Fig. 95). 29. **C. (Neotheobaldia) weindorferi** Edw.
- 49 (48). Lateral lobe of gonofurca high, reaching the apical $2/3$ of the length of the gonocoxite; long, but not strong setae present at its apex.
- 50 (51). Phallus with tiny denticles at the apex, phallus enlarged distally. On each lobe of the 9th tergite, 13-14 setae present (Fig. 89, a). Antenna slightly longer than the proboscis. 23. **C. (Neotheobaldia) drummondi** Dobrotw.
- 51 (50). Phallus without denticles at the apex, enlarged distally. On each lobe of the 9th tergite, 10-12 setae (Fig. 94, a). 28. **C. (Neotheobaldia) victoriensis** Dobrotw.

- 52 (47). Palps shorter than the proboscis; if they are equal to its length then the lateral process of gonofurca almost completely separated from the gonocoxite body.
- 53 (54). Lateral lobe of gonofurca very long, reaching the apex of the gonocoxite (index about one). Phallus distally enlarged. On each of the lobes of the 9th tergite, 9–10 setae. (Fig. 91, a) 25. **C. (Neotheobaldia) hilli** Edw.
- 54 (53). Lateral lobe of gonofurca reaches only the apical one-third of the gonocoxite (index $2/3$ but does not descend beyond it. Phallus oval or egg-shaped, without distal enlargement.
- 124 55 (56). On each lobe of the 9th tergite, only one or two strong setae. Most of the length of the lateral lobe of gonofurca fused with the gonocoxite (Fig. 92, a) 26. **C. (Neotheobaldia) otwayensis** Dobrotw.
- 56 (55). Lateral lobe of the gonofurca set off from gonocoxite throughout its length. Each lobe of the 9th tergite bears 4–7 (up to 10) setae (Fig. 96, a) 2. Genus **Austrotheobaldia** Dobrotw.
(The genus consists of a single species—**A. littleri** Tayl.).
- 57 (46). Gonocoxite with an extended terminal portion. On the gonotelopod, two digitate apical appendages. The 9th tergite very large, H-shaped, with long processes turned distally (Fig. 23). Palps shorter than the proboscis: their apices enlarged in a spatula-like form (Fig. 9, D) 4. Genus **Allotheobaldia** Brol.
(The genus consists of a single species—**A. longiareolata** Macq.)
- 58 (1). Palps very short, less than one-half of the length of the proboscis 3. Genus **Theomyia** Edw.
(The genus consists of a single species—**Th. fraseri** Edw.)

C. Fourth instar larvae

- 1 (56). Sclerotization complete, encompassing the anal segment in the form of a ring.
- 2 (55). Siphon seta occupies the proximal position on the siphon. On the head and thorax, at least some of the setae are pubescent.
- 3 (54). Antennae relatively long, slightly flexed; if they are nearly straight, not medially thickened but uniformly constricted toward the apex. At the crest of the siphon, teeth, spines or setae present, but not paired thin setae. Thin walled thoracic

air sacs and multiple-branched dendritic setae absent . . .

.....1. Genus **Culiseta** Felt.

- 4 (9). On the siphon, apart from the pairs of small proximal siphon setae, there is a ventral median row of setae; moreover, there are small setae situated dorsolaterally. Only one row of large, long scales in the comb

..... Subgenus **Climacura** H.D.K.

- 5 (8). Not more than 21 scales in the comb of the 8th segment. Not more than 10 pecten teeth on the siphon crest, the ventral median row of setae consists of not more than 6 setae.

- 6 (7). Length of the inner frontal seta not more than $1/3$ of the length of the median frontal seta. Submentum, apart from the central tooth, consists of 6–7 teeth on each side. On the siphon, the ventral median row consists of 5–6 one or two-branched setae. Fourteen setae at the common base of the ventral brush and two short setae anterior to it (Fig. 85, b and c).....20. **C. (Climacura) antipodea** Dobrotw.

- 7 (6). Length of the inner frontal seta roughly equal to half the length of the median frontal seta. In the submentum 9–10 teeth on each side. Ventral median row on the siphon consists of 4 very thin 1–2 branched setae. Twelve setae at the common base on the ventral brush and 3–4 short setae anterior to it (Fig. 88).... 22. **C. (Climacura) tonnoiri** Edw.

- 8 (5). Usually 25 large scales in the comb of the 8th segment. Over 10 pecten teeth on the siphon, crest, while the ventral median row on the siphon consists of 10–16 short multiple-branched setae (Fig. 86, c).....

.....21. **C. (Climacura) melanura** Coq.

- , 125 9 (4). The ventral median row of setae absent on the siphon. Over 25 scales in the comb and they are gathered in the form of an irregular triangular spot.

- 10 (43). Apical antennal appendages not concentrated right at the apex of the antenna (Fig. 35, 1 to 4). Body color fairly dark, not milky-white. Siphon seta usually well developed and consists of more than 3 branches. On the ventral brush, as a rule, apart from the setae set on the common base, there are more than 2 setae anterior to the common base.

- 11 (30). Antennae relatively short, without any sharp separation of the proximal (broader) and distal (narrow) portions; antennal index as a rule not more than 70% (usually not more than 50%). Mouth parts and the musculature of the labrum of mixed types (Figs. 37, 1 to 3; 39a; 40, 1 to 3; 42, 1 to 3). Siphon relatively short with index not exceeding 5. Apart

- from large pecten teeth, long setae present on the siphon crest; these long setae arranged in the same row on the siphon farther away from the apex of the siphon
- Subgenus **Culiseta** s. str.
- 12 (29). Antennae short, not more than one-half of the length of the head. Median frontal seta not more branched than the inner frontal seta. On the comb, as a rule, not more than 70 scales present.
- 13 (26). All anal gills of fairly equal length.
- 14 (17). Antennae usually shorter than one-half of the length of the head. On the comb, as a rule, less than 50 scales.
- 15 (16). Siphon short and thick: siphon index (1) not more than 3.
 1. **C.** (s. str.) **alaskaensis** Ludl.
 a (b). Postclypeal setae with three, very rarely with four branches. Color of head and siphon very dark, often almost black . . . 1a. **C. alaskaensis alaskaensis** Ludl.
 b (a). Postclypeal setae with 3-7 (usually 5-6) branches. Color of head and siphon light-brown, sometimes yellowish brown . . . 1b. **C. alaskaensis indica** Edw.
- 16 (15). Siphon relatively long and thin with an index of 3-4 . . .
 2. **C.** (s. str.) **annulata** Schr.
 a (b). Bases of the postclypeal setae at the same level as the bases of the inner frontal setae (index 0.8-1.2) (Fig. 62, a). Color of head and siphon dark (brown)
 1a. **C. annulata annulata** Schr.
 b (a). Index of postclypeal seta roughly equal to 1.5 (1.2-1.6), that is, the bases of the postclypeal setae are closer compared to the bases of the inner frontal setae (Fig. 62, b). Head and siphon light-colored (light-brown or dark ochreous) 2b. **C. annulata subochrea** Edw.
- 17 (14). Antennae usually equal to one-half of the length of the head, but not longer. On the comb, as a rule, not less than 50 scales.
- 18 (21). Branching of the median frontal seta not weaker than that of the inner frontal seta. On the comb, as a rule, over 60 scales. On the siphon crest, the number of pecten teeth is more than the number of setae.
- 19 (20). Postclypeal seta simple or forked. Outer frontal setae with not less than 15 branches. On the common base of the ventral brush, not more than 13 setae (Fig. 67, b and c).
 6. **C.** (s. str.) **impatiens** Wlk.

- 20 (19). Postclypeal seta, as a rule, with four branches (2-7). Outer frontal seta usually with 10 to 12 branches. On the common base of the ventral brush, usually more than 15 setae (13-19) (Fig. 48) 4. **C. (s. str.) bergrothi** Edw.
- 126 21 (18). Median frontal seta invariably less branched compared to the inner frontal seta. Fewer than 60 scales on the comb. On the siphon crest, the number of pecten teeth is equal to or less than the number of setae.
- 22 (21). Antennal tuft and outer frontal seta each has more than 15 setal branches. On the siphon crest, the number of pecten teeth less than the number of setae (Fig. 68, c and d) 7. **C. (s. str.) incidens** Thoms.
- 23 (22). Antennal tuft and outer frontal seta each consists of less than 15 setal branches. On the siphon crest, the number of pecten teeth usually equal to the number of setae.
- 24 (25). Postclypeal seta large, equal in length to the inner frontal seta. Lateral seta of saddle with usually more than two branches and shorter than the saddle (Fig. 73, b and c). 11. **C. (s. str.) particeps** Adams.
- 25 (24). Postclypeal seta noticeably shorter than the inner frontal seta. Lateral seta of the saddle 2-branched and equal in length to the saddle (Fig. 70, b and c) 8. **C. (s. str.) inornata** Will.
- 26 (13). Dorsal and ventral gills are of different lengths.
- 27 (28). Dorsal gills slightly longer than the ventral. Less than 10 setae in the antennal tuft. Inner frontal seta consists of not more than 8 branches; median frontal seta with not more than 5 branches. Lateral seta of the saddle 2-branched (Fig. 72, b and c) 10. **C. (s. str.) niveitaeniata** Theo.
- 28 (27). Dorsal gills noticeably shorter than the ventral. Over 15 setae in the antennal tuft. Inner frontal seta consists of more than 8 branches; median frontal seta with more than 5 branches. The lateral seta of the siphon with not more than 3 branches (Fig. 71, b and c). 9. **C. (s. str.) kanayamensis** Yam.
- 29 (12). Antennae moderately long, over one-half of the length of the head. Median frontal seta as branched or more than inner frontal seta. Usually not more than 70 scales (60 to 85) on the comb. On the siphon crest, the number of teeth is less than the number of setae (Fig. 66, b and c) 5. **C. (s. str.) glaphyroptera** Schiner.
- 30 (11). Antennae long with a fairly sharp division into proximal (up to the tuft) and distal halves; the antennal index more

than 70%, often about or more than 100%. Mouth parts and head musculature of filter type (Figs. 37, 4 and 5; 39, b; 40, 4 and 5). Siphon long, index not less than 5 (usually more than 6). Only pecten teeth are seen on the siphon crest; the row of seta in continuation of the teeth absent

..... Subgenus **Culicella** Felt.

- 31 (40). Inner frontal seta usually consists of not more than 5 branches. The comb bears not less than 120 scales; if less numerous, then the branching of the extreme upper seta posterior to the comb (seta 6) same as the extreme lower seta (13).
- 32 (31). Median frontal setae single. Not more than two setae anterior to the common base of the ventral brush (Fig. 77, b and c) 14. **C. (Culicella) inconspicua** Lee.
- 33 (32). Median frontal seta with 2-4 branches, very rarely with a single branch. Not less than 5 setae anterior to the common base of the ventral brush.
- 34 (37). Long distal teeth of the siphon more widely set and placed dorso-laterally without a specific sequence, descending beyond the center of the siphon almost to its distal one-third. Seta 5 at the base of the lateral valves of the stigmal plate flabellate (Fig. 76, b).
- 35 (36). Setae anterior to the common base of the ventral brush much shorter (by one-half) than the seta closest to it set on the common base. The median seta posterior to the comb (seta 9) very long, noticeably longer than the saddle and multiple-branched. Outer caudal seta with several branches, flabellate. 13. **C. (Culicella) fumipennis** Steph.
- 36 (35). Setae anterior to the common base of the ventral brush only slightly shorter than those next to them set at the common base. Median seta posterior to the comb (9) noticeably shorter than the saddle. Outer caudal seta with 3 branches. 18. **C. (Culicella) setivalva** Masl.
- 37 (34). On the siphon, the distal pecten teeth not set off from the proximal ones; sometimes only the distance between the two last teeth somewhat very broad. Seta 5 of the stigmal plate simple.
- 38 (39). Pecten located at the base of the siphon, not descending beyond the first one-quarter of its length. Siphon seta less than or equal to one-third of the length of the siphon (Fig. 78) 16. **C. (Culicella) morsitans** Theo.

- a (b). Index of the median frontal seta not more than 120%.
 Inner frontal seta usually with three branches (2–4).
 Usually more than 125 scales (110–160) in the comb.
 16a. **C. morsitans morsitans** Theo.
- b (a). Index of the median frontal seta more than 125[%].
 Inner frontal seta usually with 4 branches (3–6). Usually
 less than 120 scales (100–130) on the comb ...
 16b. **C. morsitans dyari** Coq.
- 39 (38). Pecten located on first one-third of the siphon length.
 Length of the siphon seta more than 1/3 of the siphon
 length 15. **C. (Culicella) litorea** Shute.
- 40 (31). Inner frontal seta consists of more than 5 branches. Less
 than 120 scales in the comb.
- 41 (42). Usually 100 or slightly more scales (80–120) on the comb.
 The branching of the extreme upper and median setae
 posterior to the comb (setae 6 and 9) as a rule identical
 while the extreme lower seta (13) invariably less branched
 than the extreme upper one. Not less than 14 setae on the
 ventral brush, the setae set on the common base (Fig. 79,
 a and b) ... 17. **C. (Culicella) nipponica** La Casse and Yamag.
- 42 (41). Scales less than 100 on the comb. The extreme upper seta
 posterior to the comb less branched compared to the me-
 dian, but roughly identical to the extreme lowermost seta.
 Not more than 13 setae on the ventral brush, the setae set
 on a common base (Figs. 81, b; 83, c)
 19. **C. (Culicella) silvestris** Sching (Shing.).
- a (b). Antennae usually of the same length as the head.
 Antennal tuft consists of less than 20 setae
 19b. **C. silvestris minnesotae** Barr.
- b (a). Antennal tuft with more than 20 setae; if less, then
 the lateral seta of the saddle invariably simple. Anten-
 nae usually shorter than the head.
- c (d). Siphon seta moderately long, usually equal to 1/3 of
 the length of the siphon. Seta *f* of the stigmal plate
 usually with a sharp flexure or bend
 19c. **C. silvestris ochroptera** Peus.
- d (c). Siphon seta short, its length usually equal to 1/4 of
 the siphon length. Seta *f* of the stigmal plate bent
 uniformly as an S.
- e (f). Median seta posterior to the comb (9) usually with
 7 branches (5–8)
 19d. **C. silvestris silvestris** Sching (Shing.).

- f (e). Median seta posterior to the comb usually with 8–10 (5–12) branches . . . 19a. **C. silvestris amurensis** Masl.
- 128 43 (10). Apical, antennal, skeletal structures concentrated right at the apex of the antenna (Fig. 35, 5 to 7). Body color milky-white, while the more sclerotized portions are yellowish; if darker, then the antennal tuft has no more than 5 branches, no more than 60 scales on the comb and no more than 5 pecten teeth on the siphon Subgenus **Neotheobaldia** Dobrotw.
- 44 (45). Color of the head and siphon brownish. Not more than 5 setae in the antennal tuft. Not more than 60 scales on the comb. Not more than 5 pecten teeth on the siphon. Lateral seta of the saddle invariably with 2 branches and shorter than the saddle. On the common base of the ventral brush usually more than 15 setae present with 1–2 setae anterior (Fig. 92, b and c) 26. **C. (Neotheobaldia) otwayensis** Dobrotw.
- 45 (44). Color of the head and siphon pale yellowish; body milky-white. Not less than 5 setae in the antennal tuft, usually many more. Not less than 80 scales on the comb. Not less than 8 pecten teeth or spines on the siphon. Not more than 15 setae at the common base of the ventral brush and those anterior to it absent.
- 46 (47). Antennal tuft consists of more than 16 setae. Median frontal seta with a single branch and the inner with not more than 3 branches. Siphon seta small, with multiple branches. Similar small, multiple-branched and absolutely identical setae posterior to the comb and the lateral seta of the saddle. Siphon long, index more than 8. (Fig. 89, b and c) 23. **C. (Neotheobaldia) drummondi** Dobrotw.
- 47 (46). Not more than 16 setae in the antennal tuft. Median frontal seta with at least two branches and the inner one with not less than 4 branches. Siphon seta with one or two branches. Setae posterior to the comb not identical. Siphon index less than 8.
- 48 (49). Antennae relatively short, noticeably shorter than the head, with index not exceeding 80%. Lateral seta of the saddle in the form of a tiny multiple-branched tuft. Siphon index usually 6–7 (Fig. 93, b and c) 27. **C. (Neotheobaldia) sylvanensis** Dobrotw.
- 49 (48). Antennae long, same length as the head. Lateral seta of the saddle with 2–5 branches. Siphon index not more than 6.

- 50 (53). Antennal tuft consists of not more than 10–12 setae. Median frontal seta with not more than 3 branches. Extreme upper (6) and median (9) setae posterior to the brush with identical branching (3–4).
- 51 (52). The median frontal seta with not more than 4 branches. Siphon seta with two branches (Fig. 91, b and c) 25. **C. (Neotheobaldia) hilli** Edw.
- 52 (51). The median frontal seta with 4–5 branches. Siphon seta with a single branch . . . 24. **C. (Neotheobaldia) frenchi** Theobald.
- 53 (50). Antennal tuft with 14–16 setae. Median frontal seta with two branches. Extreme upper seta posterior to the brush (6) more branched (4–5 branches) than the median (9) consisting of 2–3 branches (Fig. 94, b and c) 28. **C. (Neotheobaldia) victoriensis** Dobrotw.
- 54 (3). Antennae short, straight, slightly thickened medially, with highly plumose seta and relatively less branching of antennal tuft (Fig. 97, a). A pair of prominent thin-walled air sacs present in the thorax. Among the usual thoracic setae are small, dendritic setae. Siphon and saddle very heavily sclerotized, almost black. Dorsal gills longer than the ventral ones (Fig. 97, b)..... 3. Genus **Theomyia** Edw. (The genus consists of a single species—**Th. fraseri** Edw.)
- 129 55 (2). All body setae without pubescence. Siphon seta at the center of the siphon, simple. Small triangular pecten teeth on the siphon, not reaching the siphon seta (Fig. 96, b and c) . . . 2. Genus **Austrotheobaldia** Dobrotw. (The genus consists of a single species—**A. littleri** Tayl.)
- 56 (1). A ring of dorsal plates hides the anal segment only dorso-laterally (Fig. 98, d). Head heavily sclerotized, almost black, with small, almost straight antennae, on which is set a weak antennal tuft. Siphon short with the index usually less than 2. On the siphon, the distal spiny pecten teeth more widely spaced and descend without a definite sequence dorso-laterally almost to the apex of the siphon. Dorsal gills slightly longer than the ventral. (Fig. 98, c and d)..... 4. Genus **Allotheobaldia** Brol. (The genus consists of a single species—**A. longiareolata** Macq.)

Subtribe CULISETINA Maslow (Maslov, 1964a)

Adult mosquitoes have spiracular setae, but post-spiracular ones absent (Fig. 13). Radial setae with the exception of *Theomyia* Edw.

(Fig. 19). In the fourth instar larva, apart from the subgenus *Climacura* H.D.K. and the genus *Austrotheobaldia* Dobrotw., there is only one pair of siphon setae placed proximally.

1. Genus *CULISETA* Felt (1904)

Culiseta: Felt, 1904: 391c; Dyar, 1905: 107; Matheson, 1944: 220; Carpenter and La Casse, 1955: 82; Stone, Knight and Starcke, 1959: 218; Maslov, 1964a: 198. *Theobaldia*: Neveu-Lemaire, 1902: 1331; Edwards, 1932a: 101; Matheson, 1929: 177; Martini, 1929-1931: 200; Monchadskii, 1936: 188, 1951: 115; Shtakel'berg, 1937: 88. *Culicada*: Felt, 1904: 3918 [391 b] (partly). *Culicella*: Felt, 1904: 391c. *Ecculex*: Felt, 1904: 391c (partly). *Melanoconion*: Theobald, 1903: 238 (partly). *Leptosomatomyia*: Theobald, 1905: 23 (partly). *Theobaldinella*: Blanchard, 1905: 390. *Chrysoconops*: Goeldi, 1905: 114 (partly). *Climacura*: Howard, Dyar and Knab, 1915: 452. *Mochlostyrax*: Dyar and Knab, 1906: 223 (partly). *Neomelanoconion*: Theobald, 1907: 514. *Pseudotheobaldia*: Theobald, 1907: 150 and 271.

Adult mosquito. The palps of the males longer than the proboscis, or in any case not shorter than it; their apical two segments with dense setae. Radial setae as a rule well developed (Fig. 19)*. Anterior pronotal lobe usually with setae and scales; postspiracular setae and scales absent. In the females, the 8th sternite is of normal structure, without prominent lobes (Fig. 25). Legs uniformly dark-colored or with light-colored rings but without a punctate pattern. Hypopygium shown in Fig. 23. Gonocoxites of usual form like an elongated cone. Second segment of gonopod (gonotelopod) with a single digitate appendage. Ninth tergite without elongated processes. Tenth sternite in the form of two flexed plates with 2-5 teeth at the apex.

Fourth instar larva. The siphon is either long (index exceeding 5) or relatively short (index less than 5) with a single pair (except in the subgenus *Climacura* H.D.K.) of setae placed proximally and with a fairly well developed pecten. Saddle complete, encircling the anal segment like a ring. The inner caudal seta with multiple branches, outer ones simple or more often with 2-3 branches. Many setae on the head and thorax with pubescence (Fig. 31, 4, 24 and 26).

*With the exception of *Theomyia*, there are also setae situated ventrally at the base of the subcostal vein [Editor].

Subgenus *Culiseta* Felt (1904)

Culiseta: Felt, 1904: 391c. *Theobaldia*: Neveu-Lemaire, 1902: 1331. *Theobaldinella*: Blanchard, 1905: 390. *Pseudotheobaldia*: Theobald, 1907: 271.

Adult mosquito. Wing crossveins R-M and M-Cu usually fuse with each other (Fig. 20, c, I); if not, the distance between them does not exceed the actual length of the M-Cu. Spiracular setae invariably well developed. The hindtarsi either uniformly dark colored or with only proximal rings. The phallus in most cases is in the form of two semiconical, long, flattened, heavily sclerotized plates (Fig. 74, a).

Fourth instar larva. Head is not very broad, with moderately long, slightly flexed antennae. Antennal tuft on an average with not more than 15 setae. Median frontal setae of same type as the outer and inner ones. The median frontal setal index is less than 60%. Mouth parts of scraper or mixed feeding (scraper-filter) types (Figs. 37, 1-3; 40, 1-3; 42, 1-3). Pleural thoracic setae (Fig. 46) relatively short with many branches. Siphon of the 8th segment usually consists of about 50 scales. Siphon moderately long, its index not exceeding 4.0-4.5. Crest well developed with a regular row of long setae extending to the apex of the siphon. Anterior to the common base of the ventral brush, 2-5 setae present.

1. *Culiseta* (s. str.) *alaskaensis* Ludlow (1906)*

Theobaldia alaskaensis: Ludlow, 1906: 326.

Adult mosquito. The length of the wing is 5.0-8.5 mm and of the proboscis 2.9-4.9 mm. The proboscis and palps have mixed dark and light-colored scales. Spiracular setae numerous, usually not less than 15 (up to 23). Wings with distinct spots on the forks R and M and on the crossveins (Fig. 4, 5 and 6). Femora and tibiae with mixed dark and light-colored scales anteriorly. Tarsi with broad basal light-colored rings (Fig. 17, 3). Abdominal tergites with fairly broad basal bands of light-colored scales (Fig. 21, 6). Hypopygium shown in Fig. 59, a. The lobe of the 8th tergite with spines. The lateral lobes of gonofurca with two strong setae bent sharply at an angle. Distinct apical lobes present and densely clothed with short setae. Flattened valves of the phallus with pointed apices flexed sharply at an angle.

Fourth instar larvae (Fig. 59, b and c). The antennae are shorter

*Synonyms and the more important sources of literature have been given below while describing the diagnostic features of the subspecies.

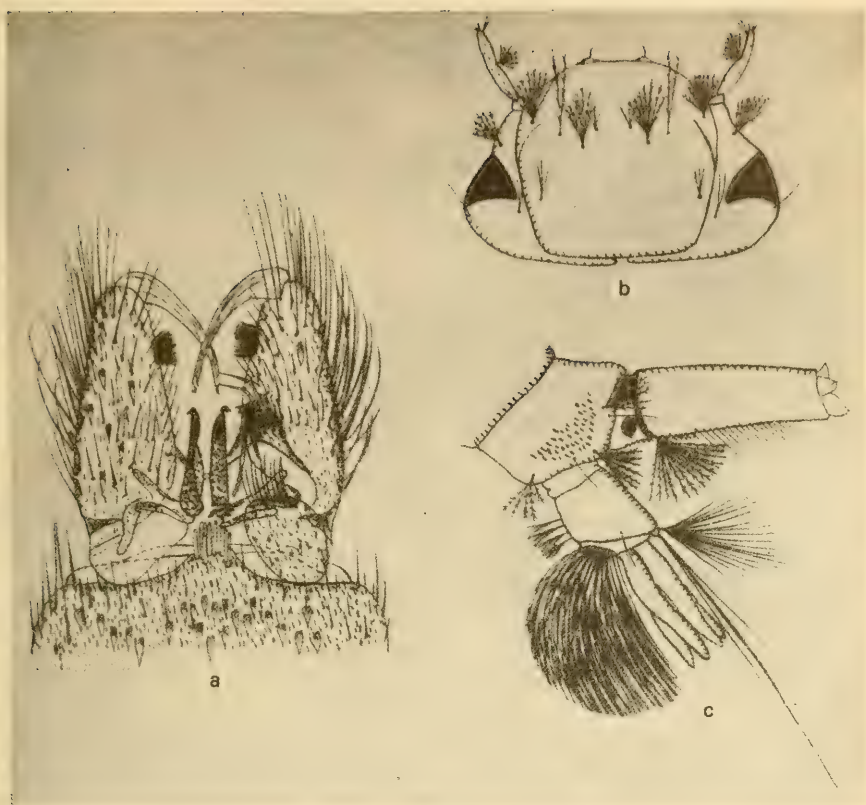


Fig. 59. *Culiseta alaskaensis alaskaensis*.

a—hypopygium of the male; b—head; c—posterior end of the 4th-instar larva.

than one-half the length of the head. The upper genal seta with many branches, usually 8–9 (6–11). The median frontal seta invariably less branched than the inner one and the latter weaker than the outer frontal seta. Mesothoracic seta 1 small and usually with many branches. The comb as a rule with 50 scales or less, although there could be more (up to 70); scales with parallel lateral margins without perceptible median constriction. The siphon is relatively short and broad: the first siphon index is usually less than 3; the second siphon index (ratio of the diameter of the base to that of the apex) less than 1.5 (usually around 1.4). Lateral seta of the saddle with 2–5 branches (usually 3), slightly shorter than the saddle.

1a. *Culiseta alaskaensis alaskaensis* Ludlow (1906)

Theobaldia alaskaensis: Ludlow, 1906: 326; Edwards, 1921a: 238, 1932a: 103; Martini, 1929–1931: 203; Matheson, 1929: 186; Monchadskii, 1930: 586, 1936: 199, 1951: 126; Shtakel'berg, 1937: 99; Natvig, 1948: 139; Marshall, 1938: 218; Edwards, Oldroyd and Smart, 1939: 17; Kramăr, 1958: 118; Maslov, 1952: 69, 1957b: 14; *Culiseta alaskaensis*: Howard, Dyar and Knab, 1915: 498; Rempel, 1950: 212; 1953: 453; Matheson, 1944: 228; Frohne, 1954a: 9; Carpenter and La Casse, 1955: 83; Gjullin, Sailer, Stone and Travis, 1961: 72; Sommerman, 1964: 1 [60]. Stone, Knight and Starcke, 1959: 218; *Culiseta alaskaensis alaskaensis*: Maslov, 1964a: 705. *Culicella alaskaensis*: Dyar, 1928: 249; *Culiseta sibiriensis*: Ludlow, 1919: 151. *Theobaldia arctica*: Edwards, 1920b: 136. *Culex annulatus*: Osten-Sacken, 1878: 18 (partly).

Adult mosquito. These have dark brown, almost black integument and dark scales in sharp contrast to the light-colored, usually pure white scales. Therefore, the mottling of the proboscis and palps, annulations of the tarsi and the light-colored bands of the abdominal tergites are in contrast. Usually only dark-colored scales with scattering of light-colored scales on the anterior veins (Fig. 3, 1 and 2). Wing spots with sharp outline (Fig. 4, 5 and 6). Hypopygium is characterized by a bend in the setae of the gonofurca; the bend is at the apical one-third portion.

Fourth instar larva. The branching of the median frontal seta does not exceed 4 (usually this seta has two branches); postclypeal seta usually with three branches (very rarely 4 branches). The siphon is relatively short with an average index of 2.6.

Distribution (Fig. 60). In the USSR, almost everywhere in the European part, to southern Crimea and Caucasus; western and eastern Siberia, trans-Baikal, Far East (absent in the southeastern Amur and to the south in the basin of the Ussuri River and southern Primorye); northern, central and eastern Europe; northeastern China, Canada and USA (Alaska, northern states and the hills of the southwest).

132 *Biology*. Mostly forest mosquitoes found as frequently in the hills as in the plains within the range, very rarely reported from human habitations. The preimaginal phases are eurytopic; most often found in rather small, usually in quite well-defined pools in the north with iso- or hyperthermal conditions and in the southern half of the range with hypothermal and most often β -mesosaprobic (more rarely α -mesosaprobic) sources.

Life form I, monocylic with female diapause, is characteristic of



Fig. 60. Range of *Culiseta alaskaensis* (1) and *C. a. indica* (2).

the north, while form II, polycyclic with female diapause, is characteristic of the south in the range. These often attack man and large mammals, rarely small mammals and birds.

1b. *Culiseta alaskaensis indica* Edwards (1920)

Theobaldia indica: Edwards, 1920b: 137; Barraud, 1924: 142, 1954 [1934]: 93; Martini, 1929–1931: 204. *Theobaldia wasiliewi* Sching. (Shing.): Shingarev, 1927: 548. *Theobaldia alaskaensis wasiliewi* Sching. (Shing.): Monchadskii, 1936: 204; Shtakel'berg, 1937: 100. *Theobaldia alaskaensis indica* Edw.: Monchadskii, 1951: 129; Maslov, 1952: 69, 1957b: 14. *Culiseta (Culiseta) alaskaensis indica* Edw.: Maslov, 1963: 762, 1964a: 206. *Culiseta (Culiseta) alaskaensis wasiliewi* Sching. (Shing.): Stone, Knight and Starcke, 1959: 218. *Culiseta (Allotheobaldia) indica* Edw.: Stone, Knight and Starcke, 1959: 221.

Adult mosquito. Very light-colored, in light brown or yellowish-brown shades. Light-colored scales are usually not pure white, but yellowish as a result of which the mottling of the proboscis, tarsal annulations and abdominal bands are not distinct. The admixture of light-colored scales to the main bulk of the dark-colored ones

along the wing veins noticeable on the entire wing surface (Fig. 3, 4-6). Wing spots are not distinct. Hypopygium is characterized by a break in the setae of the gonofurca somewhat beyond their center.

Fourth instar larva. The median frontal seta usually with 4
133 branches (from 2 to 6); postclypeal seta usually with 5-6 branches (3 to 7). The siphon with an average index of 3.0 or it is very long.

Distribution (Fig. 60). In the USSR: Caucasus, Kazakhstan, Central Asia and some reports from the Ukraine; Iran, Pakistan and northern India.

Biology. These are mosquitoes of the plains in forest-free

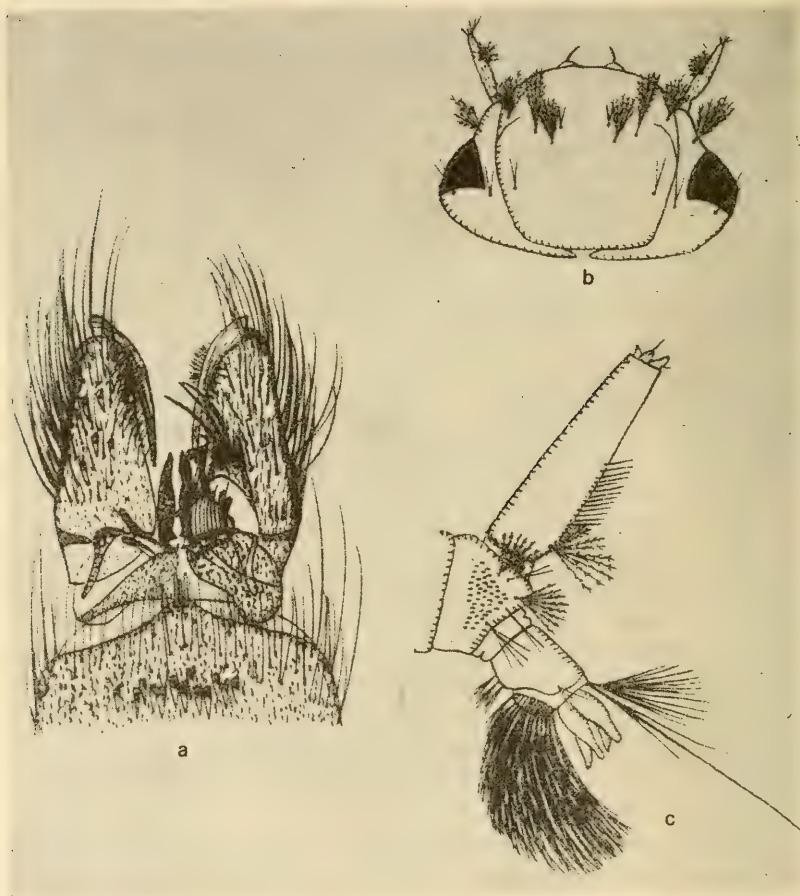


Fig. 61. *Culiseta annulata*.

a—hypopygium of the male; b—head; c—posterior portion of 4th-instar larva.

regions; found very rarely in human habitations; attacks on man are rare but attacks on domestic animals and large mammals frequent. The preimaginal phases are eurytopic. Mostly confined to small β -mesosaprobic (up to α -mesosaprobic) pools, sometimes saline (up to 1.5 per thousand). Preferred thermal range; moderate hypothermal condition; avoids shaded areas. The mosquitoes are polycyclic with female diapause (life form II).

2. *Culiseta* (s. str.) *annulata* Schrank (1776)*

Culex annulatus: Schrank, 1776: 97.

- 134 *Adult mosquito*. The length of the wing is 4.5–7.3 mm and of the proboscis 2.6–4.1 mm. Proboscis has mixed dark and light-colored scales. The palps of the females dark-colored with a light-colored apex; the palps of the males with light-colored apical basal rings on the articulations and at the center of second and third segments. Spiracular setae no less than 9 and not more than 15, usually about 10. Wings usually with distinct spots on the forks R and M and on the crossveins. Femora and tibiae anteriorly with spots or scatterings of light-colored scales; preapical rings of light-colored scales distinct on the femora. Tarsi with broad, basal light-colored rings and with a similar ring at the center of the first segment (especially distinct on the hindtarsi). Abdominal tergites with distinct, fairly broad light-colored basal bands; on the second tergite, an additional median longitudinal band of light-colored scales. Hypopygium shown in Fig. 61, a. Gonocoxite with a very few moderately long setae in the median region in the apical one-third. Lateral lobes of gonofurca with 2, 3 or more strong, uniformly flexed setae. Sclerotized valves of the phallus with straight (without bends) apices.

Fourth instar larva (Fig. 61, b and c). The antennae are shorter than one-half the length of the head. Median frontal setae less branched than the inner ones, the branching of which is less than in the outer ones. The comb usually with 50 scales (maximum 70); scales constricted in the median region and distinctly enlarged proximally. Siphon relatively long, with the index (first siphon index) exceeding 3; second siphon index usually not less than 1.5. Lateral seta of saddle small (not more than one-half of the length of the saddle) usually with three branches (2–5).

*Synonyms and the more important sources of literature have been given below while describing the diagnostic features of the subspecies.

2a. *Culiseta annulata annulata* Schrank (1776)

Culex annulatus: Schrank, 1776: 97; Fabricius, 1787: 363 (partly); Meigen, 1804: 4 (partly). *Theobaldia annulata* Schr.: Wesenberg-Lund, 1920–1921: 115; Edwards, 1921a: 288, 1932a: 103; Martini, 1929–1931: 205; Monchadskii, 1936: 204, 1951: 129; Shtakel'berg, 1937: 101; Marshall, 1938: 209; Edwards, Olyroyd and Smart, 1939: 16, Natvig, 1948: 146; Roubaud, 1952: 469; Kramář, 1953: 126; Skierska, 1955: Mihályi, Sós, Sztankay-Gulyás and Zoltai, 1956; Rioux, 1958: 199; Ruffie, 1958: 186; Senevet and Andarelli, 1959a: 249; Sicart and Ruffie, 1960. *Culiseta annulata* Schr.: Stone, Knight and Starcke, 1959: 218. *Culiseta annulata annulata* Schr.: Maslov, 1963: 764, 1964a: 106. *Culex variegatus*: Schrank, 1781: 482. *Culex affinis*: Stephens, 1825: 452. *Culex calopus*: Stephens, 1825 (partly). *Culex nicaensis*: Leach, 1825: 292. *Theobaldia maculata*: Roubaud and Colas-Belcour, 1926: 821 [871].

Adult mosquito. Usually most of the scales are dark brown, almost-black, a distinct contrast with the snow white, light-colored scales forming a pattern on the palps, proboscis, sides of thorax, abdominal tergites and on the legs. The light-colored scales are absent on the wings or a few stray ones present only on the anterior veins (Fig. 3, 1 and 2). Wing spots with sharp outline (Fig. 4, 4 and 5). Hypopygium is characterized usually by the presence of only 2 (very rarely 3) strong setae at the apex of the lateral lobe while the spines on the lobes of the 7th tergite are absent (or abundant, up to 4).

Fourth instar larva. Characterized by the placement of the bases of the postclypeal setae at the same level as the inner frontal setae (index 0.8–1.2, average 1.0) (Fig. 62, a). In the pupae (Fig. 56, 6, unlike those of *C. annulata subochrea*, denticles are usually projecting and placed in two rows along the posterior margin of the paddle.

Distribution (Fig. 63). In the USSR: western and northwestern regions of the European part, Ukraine, Crimea, Caucasus and Central Asia. Everywhere in Europe, North Africa (Morocco, Algeria and Tunisia), south to the Sahara oasis, Eritrea and Somali, Canary Islands; southwestern Asia (Asia Minor, Iraq, south to Pakistan and northern India).

Biology. These are primarily mosquitoes of forest-free regions, in the hills and plains of the range. Common in human habitations where they often attack man and domestic mammals. Attacks are common on birds and forest animals. Many investigators have reported severe sickness caused by their bites. These mosquitoes have

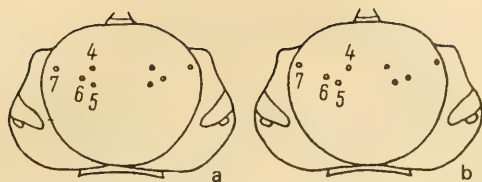


Fig. 62. Arrangement of the setae on the larval head of *Culiseta annulata* annulata (a) and *C. a. subochrea* (b). After Peus, 1930a.

been incriminated as vectors of bird malaria and chicken pox. The preimaginal phases are eurytopic and found even in saline water pools (up to 6.8 per thousand). They prefer β -mesosaprobic (to α - and even polysaprobic) sources with a moderately hypothermal range; avoid deep shade. Life forms are different in the different parts of the range: in the north, monocyclic forms with female diapause (I) are common, in the south, polycyclic with female diapause (II) and in the extreme south, polycyclic without diapause (VIII). Other life forms have been described by different investigators: IIa—polycyclic with hibernating females and males; IV—polycyclic with larval diapause and VII—polycyclic with hibernation, possibly in all growth phases.

2b. *Culiseta annulata subochrea* Edwards (1921)

136 *Theobaldia annulata subochrea*: Edwards 1921b: 198; Monchadskii, 1936: 206, 1951: 131; Petrishcheva, 1936: 49; Shtakel'berg, 1937: 103; Maslov, 1952: 69, 1957a: 35, 1961b: 57. *Theobaldia subochrea*: Edwards, 1921a: 189, 1932a: 104; Marshall, 1926: 276; 1938: 253; Martini, 1929–1931: 212; Peus, 1930a: 52; Marshall and Staley, 1936: 580; Natvig, 1948: 158; Skierska, 1955; Mihályi, Soós, Sztankay-Gulyás and Zoltai, 1956; Senevet and Andarelli, 1956a: 223, 1959a: 259, 1960: 305; Rioux, 1958: 201; Kramář, 1958: 129; Britz, 1959: 59; Coluzzi, 1960. *Culiseta subochrea* Edw.: Stone, Knight and Starcke, 1959: 220. *Culiseta annulata subochrea* Edw.; Maslov, 1963: 766, 1964a: 206. *Culex penetrans*: Robineau-Desvoidy, 1827: 407. *Theobaldia annulata ferruginata*: Martini, 1924: 438.

137 *Adult mosquito*. These mosquitoes are yellowish-brown, while the light-colored scales are not white, but pale yellowish as a result of which the pattern on the proboscis, palps, lateral thoracic regions, legs and abdominal tergites are not contrasting but diffuse. On all of the wing veins (especially on the anterior ones), there is a significant admixture of a few light-colored scales to the main body of dark-colored ones (Fig. 3, 5 and 6). Wing spots are not sharply

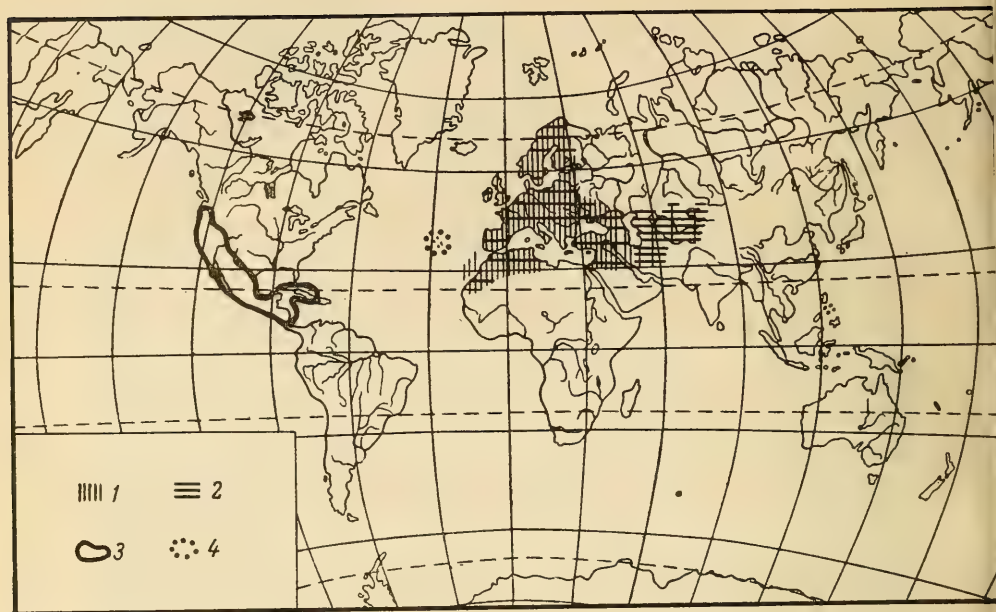


Fig. 63. Range of *Culiseta annulata annulata* (1), *C. a. subochrea* (2), *C. particeps* (3) and *C. atlantica* (4).

outlined. Hypopygium is characterized by the presence of 3 or more (very rarely 2) strong setae at the apex of the lobes, not less than 4 (0-8) spines present on the lobes of the 8th tergite.

Fourth instar larva. The bases of the postclypeal setae are closely set compared to the bases of the inner frontal setae: index 1.5 (1.2 to 1.6) (Fig. 62, b).

Pupa. The posterior margin of the paddle, unlike that of *C. a. annulata*, usually has pointed long denticles placed in a single row (Fig. 56, 8 and 9).

Distribution (Fig. 63). In the USSR: Central Asia and Kazakhstan, stray collections in the Caucasus and in the central Volga region. Everywhere in Europe; northern Africa (Morocco, Algeria, Tunisia); Asia Minor, Iran and Iraq.

Biology. These are mosquitoes of the forest-free plains. Found rarely in human habitations. Attack large mammals but rarely man. The preimaginal stages are eurytopic, found in fresh and saline (up to 3.3 per thousand), more often in β -mesosaprobic pools with moderately hypothermal or isothermal range; avoid heavily shaded zones. In the northern sections of their distribution range, polycyclic with female diapause (life form II), in the south, polycyclic without

diapause (VIII). Some investigators have also recorded life form IV, polycyclic with larval diapause.

3. *Culiseta* (s. str.) *atlantica* Edwards (1932)

Theobaldia atlantica: Edwards, 1932b: 560. *Culiseta* (?) *atlantica* Edw.: Stone, Knight and Starcke, 1959: 222. *Culiseta* (s. str.) *atlantica* Edw.: Maslov, 1963: 767, 1964a: 206.

Female. The wing length is 5–7 mm. Femora and tibiae with uniformly dark scales anteriorly situated. On the femur there is a light preapical ring. Tarsi with a broad basal, light ring. On the abdominal tergites basal bands not complete, but only the basal and lateral triangular spots of light scales are seen (Fig. 21, 11). Not much is known about the male, larva and pupa.

Distribution (Fig. 63). The Azores.

Biology. Not known.

4. *Culiseta* (s. str.) *bergrothi* Edwards (1921c)

Theobaldia bergrothi: Edwards, 1921c: 50; Natvig, 1942: 1, 1948: 160; Monchadskii, 1951: 123; Maslov, 1952: 69, 1955: 9, 1957a: 35, 1961b: 37, 1961d: 1465. *Culiseta bergrothi* Edw.: Stone, Knight and Starcke, 1956: 219; Maslov, 1961a: 865, 1961b: 51, 1961e: 616, 1962a:

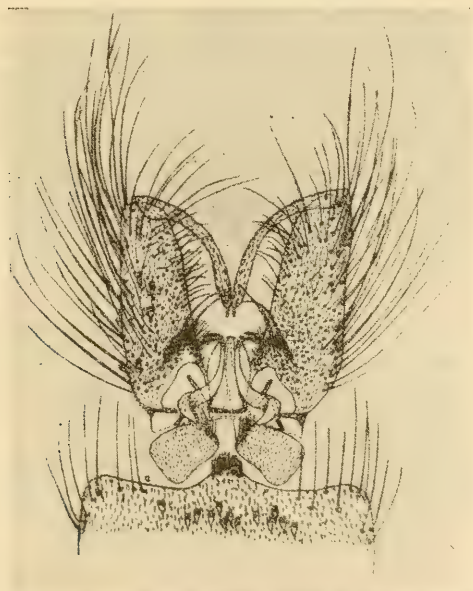


Fig. 64. *Culiseta bergrothi*, hypopygium of the male.

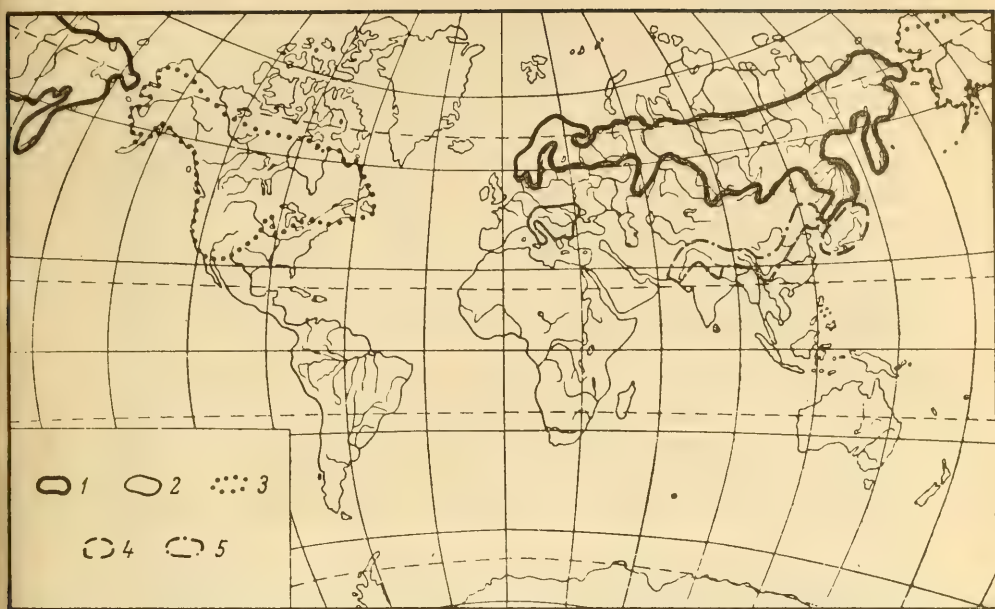
206, 1964a: 206. *Theobaldia borealis* Sching. (Shing.): Shingarev, 1927: 548; Edwards, 1932a: 103. *Theobaldia (Culicella) borealis* Sching. (Shing.): Shtakel'berg, 1937: 104, Su, 1962: 138. *Theobaldia kogiewnikowi* Sching. (Shing.): Shingarev, 1927: 547. *Culex glaphyopterus*: Schiner, 1864: 628 (partly).

Adult mosquito. The length of the wing is 4.6–7.2 mm and of the proboscis 2.2–4.2 mm. Proboscis and palps uniformly dark or with scattering of light scales. The palps of the males significantly longer than the proboscis: palpal index (ratio of the total length of the first four palpal segments to that of the proboscis) exceeds one (usually over 1.2). Spiracular setae many, but usually not more than 15 and lower sternopleural setae not more than 10. Wing spots are not distinctly manifested although distinctly discernible (Fig. 4, 2 and 3). Femora and tibiae (Fig. 17, 1) of uniform color or with a few scattered light scales. Tarsi entirely dark. Abdominal tergites with bands (Fig. 21, 5, 6, 12) or at least with lateral (Fig. 21, 11) or median (Fig. 21, 8, 9) basal spots of light scales. Hypopygium shown in Fig. 64. On the lobes of the eighth tergite, usually more than 10 (4–18) short, heavy spines. On each of the lateral lobes or gonofurca invariably two comparatively thin, uniformly flexed strong setae. Phallus weakly sclerotized, egg-shaped (Fig. 74, a). In the apical median zone of the gonocoxite, neither lateral lobes nor hairy setal groups.

Fourth instar larva (Fig. 28, 48). The antennae are usually equal to one-half the length of the head; antennal tuft variable within a wide range, but usually has more than 10 setae (5–18). The branching of the median frontal seta (4–14, average 9) is the same as of the inner frontal seta (5–13, average 10) and only slightly weaker than that of the outer frontal seta (8–17, average 10). The branching of the upper genal (2–7, average 4) and postclypeal (2–7, average 4) seta is identical. The comb usually bears more than 60 (49–98) scales. The number of teeth in the crest (10–30, average 19) is more than the number of setae (7–18, average 14). Siphon index usually about 3.5. Lateral seta of saddle usually with 3–4 branches (2 to 7). Usually 3 (3 to 5) setae anterior to the common base of the ventral brush.

Distribution (Fig. 65). In the USSR: north and west of the European parts (Estonia), northern Ural region, eastern Kazakhstan, western and eastern Siberia, Trans-Baikal and Far East, including Sakhalin; northern China; northern Europe (Finland and Scandinavia).

Biology. These are predominantly forest mosquitoes found in the hills and plains. Found rarely in association with human conditions. Attack mostly large mammals, more rarely birds; rarely attack man. In the central Amur region, they have been experimentally



138 Fig. 65. Range of *Culiseta bergrothi* (1), *C. glaphyroptera* (2), *C. impatiens* (3), *C. kanayamensis* (4), *C. niveitaeniata* (5).

infected by the microfilaria *Dirofilaria immitis*. The preimaginal stages are eurytopic, but not found in saline waters (over 1 part per thousand). Small deep, taiga groves with very well defined water surfaces with a hypothermal range (in the far north, iso- and even hyperthermal conditions) are highly typical of these mosquitoes; water is β - and α -mesosaprobic. In the far north, the mosquitoes are monocyclic with female diapause (life form I), in the south, polycyclic with female diapause (II).

5. *Culiseta* (s. str.) *glaphyroptera* Schiner (1864).

Culex glaphyropterus: Schiner, 1864: 628. *Theobaldia glaphyroptera* Schiner: Edwards, 1921a: 287, 1932a: 103; Apfelbeck, 1928: 28; Martini, 1929-1931: 209; Monchadskii, 1936: 196, 1951: 122; Shtakel'berg, 1937: 97; Natvig, 1942: 1, 1948: 160; Senevet and Andarelli, 1959a: 268; Sztankay-Gulyás, 1959: 399. *Culiseta glaphyroptera* Schiner: Stone, Knight and Starcke, 1959: 219; Maslov, 1963: 1964a: 206. *Theobaldia glaphyroptera zottae*: Ungureanu, 1956: 4.

Adult mosquito. The length of the wing is 5.0-7.1 mm and that of the proboscis 2.8-3.8 mm. Proboscis and palps uniformly dark, more rarely with scattered light scales. The palps of the males longer

than the proboscis but the palpal index is less than one. Spiracular setae numerous (16–22), usually about 20; lower sternopleural setae usually 15 (12–18). Wing spots absent (Fig. 4, 1) or faint (Fig. 4, 2). Abdominal tergites with basal bands of light scales. Femora, tibiae and tarsi with uniformly dark scales, without light rings. Hypopygium shown in Fig. 66. On the lobes of the 8th tergite, 9–12 strong, short spines. A distinct lobe at the extreme apex of the gonocoxite with a tuft of long, lanceolate appendages.

Fourth instar larva (Fig. 66). The antennae are relatively long, usually more than one-half the length of the head: index 50–70, average 59.6%. In the antennal tuft, about 10 (7–12) setal branches. Upper genal seta invariably more branched (4–7, average 6) than the postclypeal seta (2–3). The branching of the median frontal seta (5–12, average 9) almost the same as the outer seta (6–12, average 10), but noticeably greater than the inner (5–9, average 7). The comb usually has not less than 70 (60–85) scales. On the siphon crest, the number of pecten teeth (12–24, average 18) is invariably less than the

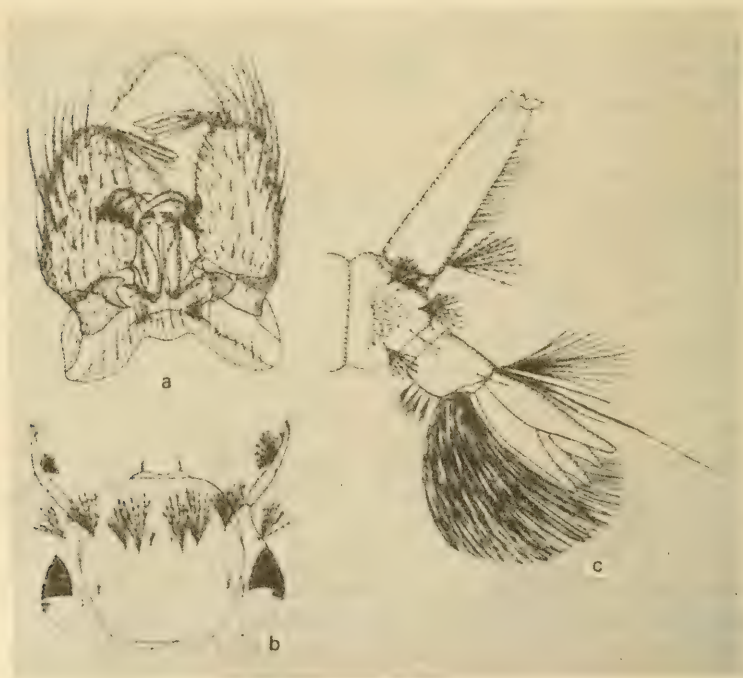


Fig. 66. *Culiseta glaphyroptera*.

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

number of setae (17–36, average 21). Lateral seta of the saddle usually with two branches, rarely three. Usually 4 setae (3–5) anterior to the common base of the ventral brush.

Distribution (Fig. 65). In the USSR, only in the Ukraine (western regions), probably in Moldavia; European part of the Mediterranean region, central and eastern Europe.

Biology. These are forest mosquitoes of hilly regions; not found in human habitations. Attack birds and wild mammals; do not attack man. The preimaginal stages are found only in small springs with stagnant or slightly flowing pools with a distinct hypothermal range and with fresh water. Monocyclic with female diapause (life form I).

6. *Culiseta* (s. str.) *impatiens* Walker (1848)

Culex impatiens: Walker, 1848: 5. *Culiseta impatiens* Wlk.: Howard, Dyar and Knab, 1915: 483; Hammon and Howitt, 1942: 163; Matheson, 1944: 226; Frohne, 1953: 103, 1954b: 10; Rempel, 1953: 454; Carpenter and La Casse, 1955: 85; Stone, Knight and Starcke, 1959: 219; Gjullin, Sailer, Stone and Travis, 1961: 73; Maslov, 1963: 771, 1964a: 206; Sommerman, 1964. *Culicella impatiens* Wlk.: Dyar, 1928: 246. *Theobaldia impatiens* Wlk.: Matheson, 1929: 183. *Culex consobrinus*: Robineau-Desvoidy, 1827: 408; Theobald, 1901a [1901]: 787, 1910: 358. *Culex pinguis*: Walker, 1866: 337. *Culex testaceus*: Van der Wulp, 1867: 128. *Culex absobrinus*: Felt, 1904: 318. *Culiseta absobrina* Felt: Theobald, 1907: 383, 1910: 322. (?) *Anopheles annulimanus*: Van der Wulp, 1867: 129.

140 *Adult mosquito*. The length of the wing is 5.0–6.0 mm and of the proboscis 2.9–3.2 mm. The palps of the female are dark with scattered light scales. In the males, the palps are somewhat longer or equal to the length of the proboscis. Wing spots faintly distinguishable (Fig. 4, 2 and 3). Femora and tibiae anteriorly dark with a fairly significant admixture of light scales (sometimes femora almost wholly light-colored); tarsi uniformly dark, without rings. Abdominal tergites with light basal bands slightly broadened in the median portion (Fig. 21, 12). Hypopygium shown in Fig. 67, a. Along the distal margin of the 8th tergite is an even row of strong spines. On each lateral lobe of the gonofurca, one heavy seta is present. On the gonocoxite is a small preapical lobe clothed in long setae among which one or a few stand out prominently in length and thickness. The phallus is weakly sclerotized.

Fourth instar larva (Fig. 67, b and c). This has relatively short antennae, the length of which is usually equal to one-half that of the



Fig. 67. *Culiseta impatiens*.

a—hypopygium of male (after Gjullin, Sailer, Stone and Travis, 1961),
b—head; c—terminal end of the 4th-instar larva.

head. The inner and median frontal setae roughly of the same length and with branches (5–7); both of these are shorter and significantly
141 less branched compared to the outer frontal setae (14–17, average 15 branches). The upper genal seta is comparatively less branched with less than 7 branches. Mesothoracic seta 1 is small, simple or forked. The comb usually has over 60 (58–73) scales. The number of pecten teeth in the crest (17–20, average 19) exceeds the number of setae (13–16, average 15).

Distribution (Fig. 65). Canada and USA (Alaska, west, southwest, north and northeast regions).

Biology. These are predominantly forest mosquitoes found in the hills and plains. Absent in human habitations. Rarely attack man or small mammals and birds, but often attack large wild and domestic mammals. The preimaginal stages are eurytopic; more characteristic of β - and α -mesosaprobic, hypothermal, heavily shaded stagnant water pools. In all parts of the range of this species the mosquitoes are monocyclic with female diapause (life form I.)

7. *Culiseta* (s. str.) *incidens* Thomson (1868)

Culex incidens: Thomson, 1868; 443. *Culiseta incidens* Thoms.: Howard, Dyar and Knab, 1915: 479; Hammon and Reeves, 1943a: 425, 1943b: 241; Cook, 1949: 7; Hubert, 1953: 207; Rempel, 1953: 455;



Fig. 68. *Culiseta incidens*.

a—wing (after Rempel, 1953); b—hypopygium of male (after Gjullin, Sailer, Stone and Travis, 1961); c—head; d—terminal end of the 4th-instar larva (after Carpenter and La Casse, 1955).

Frohne, 1954a: 9; Carpenter and La Casse, 1955: 87; Stone, 1958: 236; Stone, Knight and Starcke, 1959: 219; Gjullin, Sailer, Stone and Travis, 142 1961: 74; Maslov, 1963: 772, 1964a: 206. Matheson, 1944: 277; *Theobaldia incidens* Wlk.: Theobald, 1903: 151, 1907: 279, 1910: 275; Matheson, 1929: 185; Frost, Herms and Hoskins, 1936: 461. *Culicella incidens* Thoms.: Dyar, 1928: 247. *Culex impiger*: Walker, 1848: 6 (partly). *Culex quinquefasciatus*: Say, 1823: 10 (partly). *Culex nigripes*: Zetterstedt, 1840: 807 (partly). *Culex particeps* Adams, 1903: 26 (partly). *Culex consobrinus*: Robineau-Desvoidy, 1827: 408; Theobald, 1901: 78 (partly).

Adult mosquito. The length of the wing is 5.0–6.6 mm and of the proboscis 3.1–3.6 mm. The palps of the females dark with specks of light scales, especially numerous in the proximal half. The palps of the males invariably slightly longer than the proboscis (index 1.1–1.2), but the palpal index is invariably less than 100% (80–95, average 85%). The characteristic long spots on the wings (Fig. 68, a) represent accumulations of scales on R and M proximal to the crossveins and immediately after the forks R₂, R₃, M₁ and M₂ in this same region and at R₄₊₅. Femora anteriorly light with a dark preapical ring. Tibiae with scattered light scales, situated anteriorly, sometimes with light rings. Abdominal tergites with light basal bands broadening in the middle region (Fig. 21, 12). Hypopygium shown in Fig. 68, b. The lobe of the 8th tergite with a few (4–8, average 6) spines. On each lateral lobe of the gonofurca, 2 strong, curved setae. Gonocoxite has small preapical lobes set with long setae among which one seta is noticeably longer and thicker than the rest. The phallus relatively heavily sclerotized and falls into an intermediate position between the sclerotization typical of the subgenus *Culiseta* s. str. (Fig. 74, a) and subgenus *Culicella* (Fig. 74, b).

Fourth instar larva (Fig. 68, c and d). The antennae are relatively short, equal to one-half the length of the head. The antennal tuft with many setal branches (16–23, average 20). The branching of the median frontal seta (4–5 branches) far weaker than that of the inner 143 (8–12, average 10), the former invariably longer. The genal seta with many branches (12–15, average 13). Mesothoracic seta 1 small and simple. The comb has about 50 (40–55) scales. The number of pecten teeth on the crest (11–16, average 13) is less than the number of setae (16–22, average 18). Lateral seta of the saddle thin and small (shorter than the saddle) simple or branched (1–5, average 2 or 3).

Distribution (Fig. 69). Canada (northern and western provinces), USA (from Alaska to Texas and northwestern states) and Mexico (Baja California peninsula).

Biology. These mosquitoes are found predominantly on the plains. Common in human habitations. Attack man occasionally, but attacks on large domestic and wild mammals more frequent. Reported as mechanical vectors of tularemia and secondary vectors of eastern and western equine encephalomyelitis and St. Louis encephalitis; may be infected with and transmitters of Japanese encephalitis. The preimaginal stages are eurytopic, prefer β - and α -mesosaprobic pools. The northern zones of the range moderately thermophilic (isothermal, even hyperthermal); in the southern regions prefer pools with a distinct hypothermal regime. In the northern regions, the mosquitoes are polycyclic with female diapause (life form II); in the south, polycyclic with larval diapause (life form IV).

8. *Culiseta* (s. str.) *inornata* Williston (1893)

Culex inornatus: Williston, 1893: 253. *Culiseta inornata* Will.: Howard, Dyar and Knab, 1915: 488; Hammon and Howitt, 1942: 163; Hammon and Reeves, 1943a: 425, 1943b: 241; Hammon, Reeves, Benner and Brookman, 1945: 1133; Rees and Onishi, 1951: 233; Matheson, 1944: 225; McLintock, 1952: 195; Rempel, 1953: 451; Car-

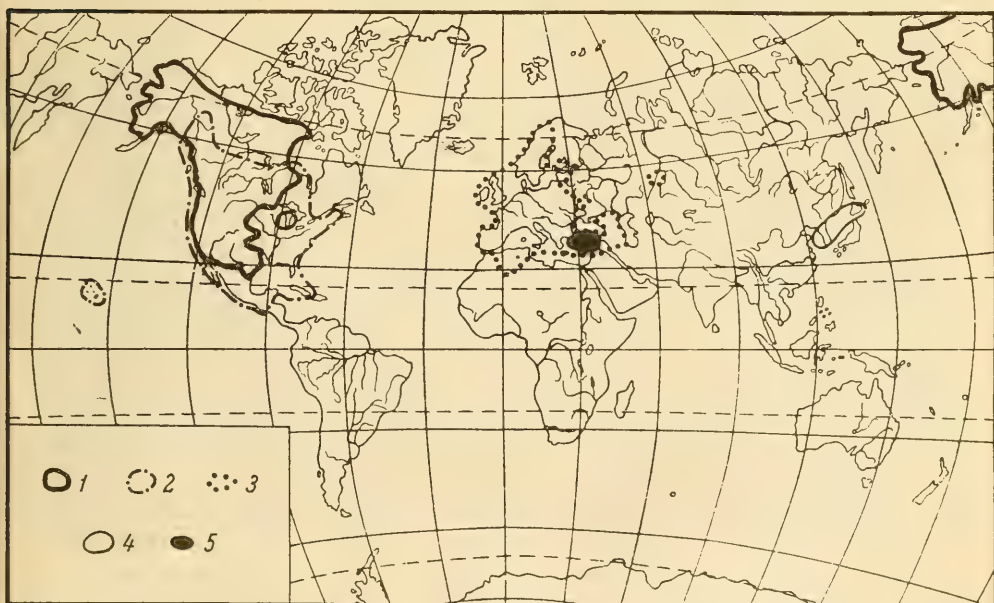


Fig. 69. Range of *Culiseta incidens* (1), *C. inornata* (2), *C. fumipennis* (3), *C. nipponica* (4), *C. setivalva* (5).

penter and La Casse, 1955: 89; Hess and Holden, 1958: 294; Barr, 1959: 47; Feir, Lengy and Owen, 1961: 13; Maslov, 1963: 775, 1964a: 206. *Culicella inornata* Will.: Dyar, 1924b: 245. *Theobaldia inornata* Will.: Matheson, 1929: 182, Ripstein, 1935: 63; Owen, 1942: 903. *Culex consobrinus*: Robineau-Desvoidy, 1827: 408; Theobald, 1901: 78, 1910: 358. *Culex absobrinus*: Felt, 1904: 318 (partly). *Culiseta absobrina* Felt: Theobald, 1907: 383, 1910: 322 (partly). *Culex magnipennis* Felt: Theobald, 1907: 383, 1910: 322 (partly).

Adult mosquito. The length of the wing is 3.5–6.4 mm and of the proboscis 2.6–4.2 mm. The palps of the females dark with specks of light scales. In the males palps invariably longer than the proboscis (index 1.1–1.25, average 1.16) and the palpal index close to 100% (90–105, average 95.7%). Spiracular setae many, but not more than 10–12. Wing spots absent (Fig. 4, 1). Femora, tibiae and the first two tarsal segments with fairly significant speckling of light scales, often almost entirely light, but without rings. Abdominal tergites with light basal bands, noticeably enlarged laterally (Fig. 21, 12); a median, distally narrow longitudinal band of light scales is seen on the second tergite. Hypopygium shown in Fig. 70, a. Lobes of the 9th tergite heavily sclerotized along the apical margin and set with short, thick spines. Lateral lobe of gonofurca without strong setae. The phallus typical of *Culiseta* s. str. forms.

Fourth instar larva (Fig. 70, b and c). The antennae roughly measure one-half the length of the head. In the antennal tuft, usually less than 15 setal branches (11–17, average 13). The median frontal setae with less branches (3–6) than the inner (6–9, average 7) and noticeably shorter than it. Upper genal seta with many
144 branches, but the number of branches is less than 12 (8–11, average 9). Mesothoracic seta 1 weak, simple. The comb has about 50 scales (40–60, average 46.6). The number of pecten teeth on the crest (11–20, average 15) and setae (10–18, average 15) is similar. The lateral seta of the saddle is comparatively strong and long, equal to the length of the saddle.

Distribution (Fig. 69). Canada, USA (Alaska and almost all of North America), Mexico, Cuba and the Hawaiian islands*.

Biology. These mosquitoes are predominantly characteristic of the hills and plains of forest-free regions. Rarely found in human habitations. Often attack man and domestic animals. Reported as additional vectors of American encephalitides (eastern, western and

*The Hawaiian Islands is an erroneous listing based upon a single interception from an aircraft arriving in Hawaii, see Hughes (1961: 99) [Editor].

St. Louis); quite recently, a new pathogenic virus of group "Cache Valley Virus" (Holden and Hess, 1959) was isolated from these mosquitoes in the northern regions of Utah. These mosquitoes have been experimentally infected with Japanese encephalitis virus and by the microfilaria of *Wuchereria bancrofti* (without completion of the cycle) and causative organisms of bird malaria. The preimaginal stages are eurytopic with a preference for β - and α -mesosaprobic pools. In the northern regions, moderately thermophilic; in the southern regions, moderately psychrophilic. In the north, the mosquitoes are polycyclic with female diapause; in the southern regions of the range, polycyclic without diapause.

9. *Culiseta* (s. str.) *kanayamensis* Yamada (1932)

Theobaldia kanayamensis: Yamada, 1932: 218; La Casse and Yamaguti, 1950: 80; Ch'in 1959: 272; Su, 1962: 138. *Culiseta kanayamensis* Yam.: Stone, Knight and Starcke, 1959: 219; Maslov, 1963: 777, 1964a: 206.

Adult mosquito. The length of the wing is 5.5–6.0 mm. The palps of the females dark with areas of light scales. The palps of the males only slightly longer than the proboscis. Wing spots distinct

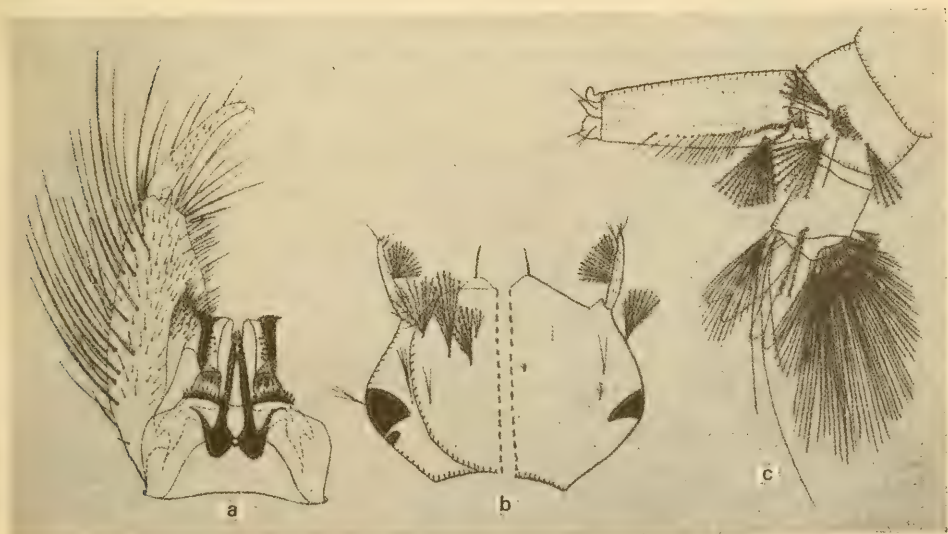


Fig. 70. *Culiseta inornata* (after Carpenter and La Casse, 1955).
a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

(Fig. 4, 3) although not sharp. Femora and tibiae with areas of light scales situated anteriorly. Tarsi entirely dark, without rings. Abdominal tergites with bands, slightly constricted in median portion. Hypopygium shown in Fig. 71, a. On the lobes of the 8th tergite, 10-13 spines. Lateral lobes on gonofurca with 2-3 uniformly flexed setae which are not very thick. On the lobes of the 9th tergite more than 10 setae. The phallus lightly sclerotized with a slightly broadened and flat (perpendicular to the longitudinal body axis) apex.

Fourth instar larva (Fig. 71, b and c). Antennal tuft with numerous (15-25) branches. The median frontal seta less branched (6-9) than the inner (8-13). Postclypeal seta with 3-5 branches. The comb has 50 to 100 scales. The upper seta posterior to the comb (6) with many branches (4-10); the median seta (9) is even more branched with 7-14 branches. The number of pecten teeth on the crest (15-22) is invariably more than the number of setae (9-16). The siphon seta usually with more than 8 (7-11) branches. The lateral seta of the saddle has 3-4 branches. On the common base of the ventral brush, 17-18 setae and anterior to the common base 3-4 setae. Dorsal gills shorter than the ventral.

Distribution (Fig. 65). Japan and Korean Peninsula.

Biology. These are forest mosquitoes, found in the hills and plains. Not recorded from human habitations, but attack man and large mammals close to the reported breeding sites. The preimaginal

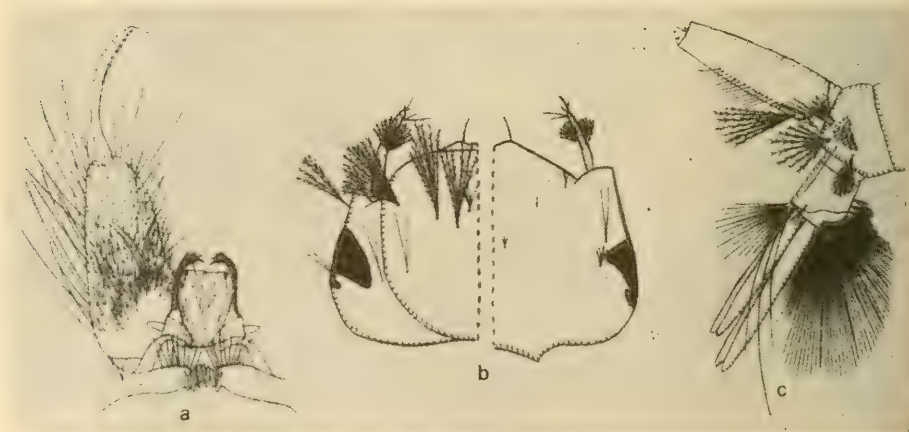


Fig. 71. *Culiseta kanayamensis* (after La Casse and Yamaguti, 1950).
a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

stages are found in small pools of springs with fresh water and a hypothermal regime. Life forms not established.

10. *Culiseta* (s. str.) *niveitaeniata* Theobald (1907)

Pseudotheobaldia niveitaeniata: Theobald, 1907: 272, 1910: 270. *Theobaldia niveitaeniata* Theo.: Barraud, 1924: 14, 1934: 91; Shtakel'berg, 1937: 98. *Culiseta niveitaeniata* Theo.: Stone, Knight and Starcke, 1959: 219; Maslov, 1963: 778; 1964a: 206. *Theobaldia kanayamensis* Yam.: Liu and Feng, 1956: 335. *Theobaldia sinensis*: Meng and Wu*, 1962: 382.

146 *Adult mosquito*. The length of the wing is 5.4–7.5 mm and of the proboscis 3.0–4.4 mm. The palps of the females dark with scattered light scales. The palps of the males roughly the same length as the proboscis (0.95–1.1, average 1.0). Spiracular setae numerous, but usually less than 10 (5–13, average 9); lower sternopleural setae usually 10 or more (9–13, average 11). Scutellum covered with broad, lanceolate white scales. Wing spots faintly distinguishable (Fig. 4, 2). Tarsi uniformly dark, without ringlets. Abdominal tergites with light basal bands constricted in the middle (Fig. 21, 12); bands on the 5th–7th segments usually interrupted and the light pattern is in the form of basal-lateral triangular spots (Fig. 21, 11). Hypopygium shown in Fig. 72, a. Eighth tergite without spines. On each lobe of the 9th tergite, 7–11 setae. On each lateral lobe of the gonofurca, 2 strong setae sharply bent at an angle. A bulging lobe on the gonocoxite far from its apex with a tuft of long hairy appendages. Appendage of gonoteloped simple or doubled, giving the impression of two appendages.

Fourth instar larva (Fig. 72, b and c). The antennae are usually shorter than one-half the length of the head (30–60, average up to 40%). Antennal tuft relatively less branched (3–8, average 5). Median frontal seta far less branched (2–5, average 4) compared with the inner (4–8, average 6) and outer (4–10, average 7) frontal seta. The comb usually has 50 (30–70) scales. The extreme upper seta posterior to the comb (6) less branched (2–5, average 3), as the extreme lower one (3–4); median (9) with many branches (8–12, average 10). Siphon seta usually has not more than 8 branches (4–11, average 9). The

*The comparative data given (Meng and Wu, 1962, pp. 386 and 387) for *Theobaldia sinensis* sp. nov., *Th. niveitaeniata* Theo. and *Th. kanayamensis* (nec. Yamada) Liu and Feng suggest that it is impossible to separate *Th. sinensis* as a new species and it is necessary to consider this name as well as *Th. kanayamensis* (in the description of Liu and Feng, 1956, see Maslov, 1963 and 1964a) under synonymy with *Culiseta niveitaeniata* Theo.

number of pecten teeth on the siphon crest (10–18, average 15) slightly more than that of the row of setae (8–20, average 13). The lateral seta of the saddle has 2 branches. On the common base of the ventral brush (11–15, average 13) setae and anterior to it 2–4 setae. Dorsal gills slightly longer than the ventral.

Distribution (Fig. 65). Northern India, northeastern, central and southern China.

Biology. These mosquitoes are found in the forest-free regions of the hills. Not found near human habitation. The victims of their attack not known. The preimaginal stages found in spring pools with fresh water and a hypothermal range. The life forms have been identified: IV—polycyclic with larval diapause and VIII—polycyclic without the essential diapause (southern China).

11. *Culiseta* (s. str.) *particeps* Adams (1903)

Culex particeps: Adams, 1903: 26. *Culiseta maccrackenae*: Dyar and Knab, 1906 [1906a]: 133; Howard, Dyar and Knab, 1915: 494; Dyar,

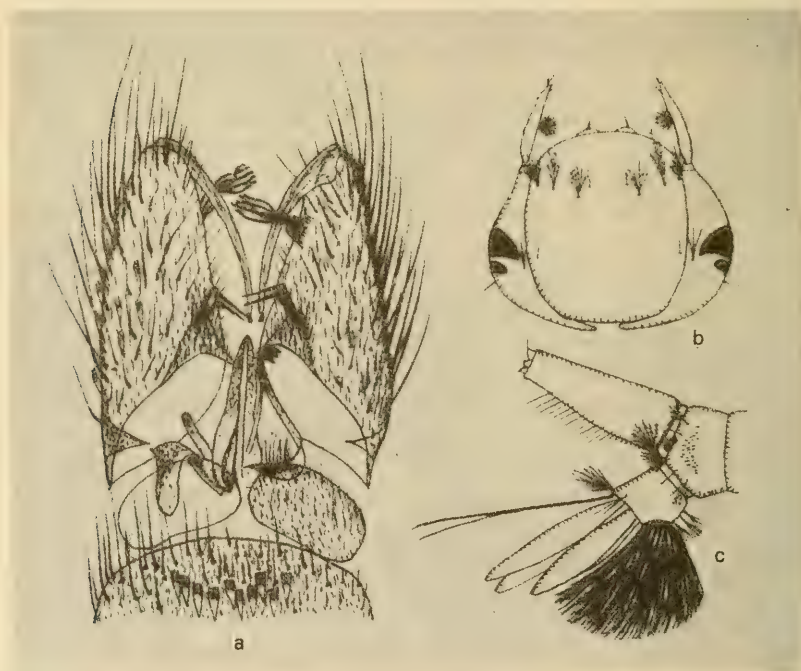


Fig. 72. *Culiseta niveitaeniata*.

a—hypopygium of the male, b—head; c—terminal end of the 4th-instar larva.

1924a: 144; Matheson, 1944: 229; Carpenter and La Casse, 1955: 9. *Theobaldia maccrackenae* Dyar: Ripstein, 1934: 249. *Culicella maccrackenae* Dyar: Dyar, 1924b: 248. *Culiseta particeps* Adams: Stone, 1958: 236; Stone, Knight and Starcke, 1959: 219; Gjullin, Sailer, Stone and Travis, 1961: 75; Maslov, 1963: 779; 1964a: 206, *Culiseta dugesi*: Dyar and Knab, 1906 [1906a]: 134. *Culex annulatus*: Fabricius, 1787: 363 (partly). *Culex annulatus*: Meigen, 1804: 4.

Adult mosquito. The length of the wing is 5.0–5.5 mm. The palps of the females with light rings, with light scales and a similarly light apex. Wing spots distinct (Fig. 4, 4 and 5). Femora and the anterior tibiae with dark scales with a fairly significant admixture of disseminated light scales situated anteriorly. Femora with light preapical annulation. Mid- and hindtibiae with a broad longitudinal band of light scales or entirely light scales situated anteriorly



147 Fig. 73. *Culiseta particeps* (after Carpenter and La Casse, 1955).
a—hypopygium of the male; b—head; c—terminal end of the 4th instar larva.

(Fig. 17, 2). Tarsi with broad basal light rings. Abdominal tergites with basal transverse light bands. Hypopygium shown in Fig. 73, a. Lobe of the 8th tergite with one short stout spine. Lateral lobe of gonofurca with three heavy setae. In the median-apical one-third of the gonocoxite, a small, enlarged lateral lobe with long setae.

Fourth instar larva (Fig. 73, b and c). Antennae roughly equal to one-half the length of the head. Median frontal seta far less branched (3-4) compared to the inner (8 branches), while the posterior is slightly weaker compared to the outer (10-12 branches) frontal seta. Postclypeal seta consists of 3-5 branches; it is very long, equal in length to the inner frontal seta. Mesothoracic seta 1 with 2-4 branches, large. On the siphon crest, the number of pecten teeth (12-18) is the same as the number of setae (10-12). Saddle with a distinct group of short spinules along the distal margin dorsally; lateral seta with 1-5 branches, noticeably shorter than the saddle.

Distribution (Fig. 63). USA (Oregon, California, Nevada, Utah and Arizona), Mexico, Central America and Cuba.

Biology. These mosquitoes are found in forest-free regions in the plains. Rarely found in a human environment. Attacks on man not reported, but often attack domestic animals. Polycyclic with the female hibernating.

Subgenus *Culicella* Felt (1904)

Culicella: Felt, 1904: 391c. *Culicada*: Felt, 1904: 391c.

Adult mosquito. Colored brownish, usually with a fairly significant admixture of light scales. Crossvein m-cu located proximal to R-M, usually at a distance twice that of the length of the m-cu itself (Fig. 20, c, 2). Spiracular setae distinctly developed as in *Culiseta* s. str. Hindtarsi with narrow apical ring near the joints or only with apical rings. The phallus of the hypopygium (Fig. 74, b) in most instances weakly sclerotized and egg-shaped.

Fourth instar larva. Has a broad head (Fig. 34), long, often sharply flexed antennae, multiple branched antennal tuft. Median frontal seta simple or with very few branches, long or even very long, with the index exceeding 100%. Mouth parts adapted for filter type feeding (Fig. 37, 40, 42). Pleural setae of thorax (Fig. 47) very long and relatively weakly branched. The comb of the 8th segment usually with numerous (not less than 60-70, often 100 or more) scales. Siphon long, with an index not less than 4.5-5.0. Crest small, usually placed at the very base of the siphon and not continuing in the form of a row of setae. Seta anterior to the common gill base invariably

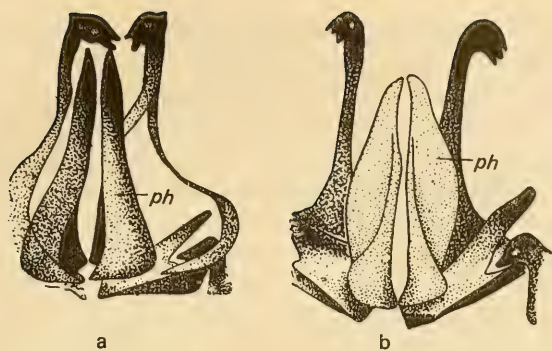


Fig. 74. Phallus (*ph*) of hypopygium typical of the males of the subgenus *Culiseta* s. str. (a) and *Culicella* (b).

very well developed and with many branches; usually these are not less than 5.

12. *Culiseta* (*Culicella*) *atra* Lee (1944)

Theobaldia atra: Lee, 1944: 220. *Culiseta* (?) *atra* Lee: Stone, Knight and Starcke, 1959: 222. *Culiseta* (*Culicella*) *atra* Lee: Maslov, 1963: 781, 1964a: 212.

Adult mosquito. The palps of the males longer than the proboscis by one-half the length of their last segment. Spiracular setae few, not more than 4, but strong and dark. On each lobe of the scutellum, 6-7 long marginal setae. Tarsal segments of all legs completely dark. Abdominal tergites dark, without bands (Fig. 21, 1). Three or four setae on each lobe of the 9th tergite of the hypopygium. Strong setae absent on the lateral lobes of the gonofurca, the height of the lateral lobes not reaching the center of the gonocoxite. Phallus egg-shaped. The preimaginal stages have not been found*

Distribution (Fig. 75). Western Australia.

Biology. Not known.

13. *Culiseta* (*Culicella*) *fumipennis* Stephens (1825)

Culex fumipennis: Stephens, 1825: 453; Theobald, 1910: 296. *Theobaldia fumipennis* Steph.: Edwards, 1921a: 290, 1932a: 105; Martini, 1929-1931: 216; Marshall and Staley, 1933: 119; Monchad-

*The larvae and pupae have been subsequently described. See Dobrotworsky, N.V. 1968, notes on *Culiseta* (*Culicella*) *atra* (Lee) (Diptera: Culicidae) in Western Australia, *J. Austr. Ent. Soc.*, 7: 11-14 [Editor].

skii, 1936: 209, 1951: 133; Shtakel'berg, 1937: 110; Marshall, 1938: 220; Edwards, Oldroyd and Smart, 1939: 18; Natvig, 1948: 180; Rioux 1958: 209; Ruffie, 1958: 195; Senevet and Andarelli, 1959a: 281. *Culiseta (Culicella) fumipennis* Steph.: Stone, knight and Starcke, 1959: 220; Maslov, 1963: 782; 1964a: 212. *Culex ficalbii*: Noe, 1899: 238; Theobald, 1901: 335. *Theobaldia ficalbii* Noe: Theobald, 1910: 271. *Culicada theobaldii*: Meijere, 1911: 143. *Culex cantans*: Meigen, 1818: 4 (partly). *Culex maculatus*: Meigen, 1804: 4(partly).

Adult mosquito. The length of the wing is 5.6–7.0 mm and that of the proboscis 3.0–3.7 mm. Proboscis with a significant number of scattered light scales sometimes forming a longitudinal white line. The palps of the males longer than the proboscis due to the length of the last segment (palpal index over 100%). Spiracular setae numerous (9–13, average 10.4); lower sternopleural setae less than 10 (7–9): preepimeral not more than 6 (usually 5). The tarsi with light rings on all joints (Fig 17, 5). Abdominal tergites with basal-lateral spots of light scales (without complete bands) (Fig. 21, 11). On the abdominal sternites the characteristic pattern of dark scales on the form of the letter V with the pointed end turned anteriorly is visible (Fig. 21, 20). Hypopygium shown in Fig. 76, a. On the lobes of the 8th tergite



Fig. 75. Range of *Culiseta atra* (1), *C. inconspicua* (2), *C. litorea* (3), *C. morsitans morsitans* (4), *C. m. dyari* (5).

some spines are seen. Gonocoxite relatively long. Index not less than 2.5, usually over 3. On each lateral lobe of the gonofurca, 3–4 heavy setae. The base of the gonotelopod gradually enlarged, not broadening suddenly.

Fourth instar larva (Fig. 76, b). The comb bears over 120 scales; the median seta posterior to the comb (9) very long, much longer than the saddle. Only 12–16 pecten teeth on the siphon; some of the longer ones are set off and scattered at random along the siphon and descend beyond its center, but do not reach the distal one-third portion. Siphon seta consists of 4–5 branches, the length of which is equal to or exceeds one-half of the length of the siphon. Seta 5 at the base of the lateral valve of the stigmal plate flabellate. Outer caudal seta in the form of a flabellum [brush] with many branches
 151 (average 6 branches). Anterior to the common base of the ventral brush, 7–9 setae present which are much shorter than the setae next to them on the common base of the ventral brush.

Distribution (Fig. 69). In the USSR, northern and western European parts, Ukraine, Caucasus, central Urals and southwestern Siberia; northern, western and eastern Europe; everywhere in the

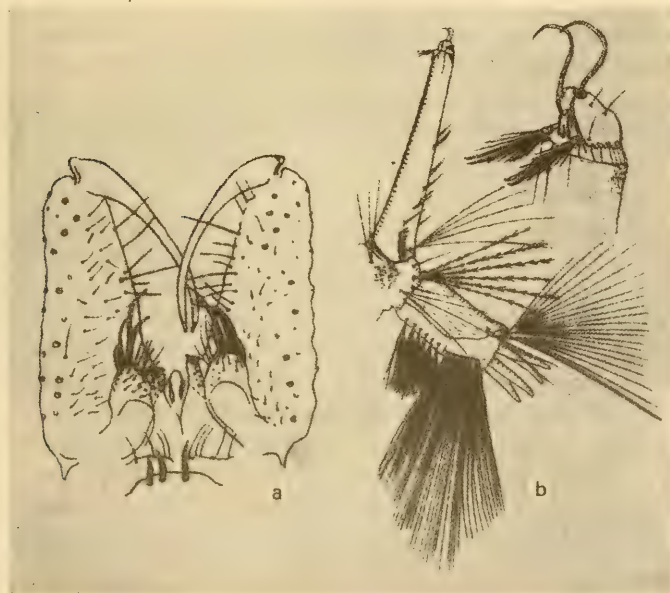


Fig. 76. *Culiseta fumipennis*.

a—hypopygium of the male (after Natvig, 1948) and b—terminal end of the 4th-instar larva (after Seguy, cited by Monchadskii, 1951).

European part of the Mediterranean; Asia Minor and northern Africa (Algeria).

Biology. These mosquitoes are found in forest-free regions in the plains. Not found near human habitations and do not attack man (only a few stray instances reported); the victims of their blood meal are birds and wild mammals. The preimaginal stages develop in fairly open, unshaded, isothermal, oligo-, β - and more rarely α -mesosaprobic pools. Among its life forms we know of the monocyclic mosquitoes with larval diapause (III), monocyclic with female diapause (I—in northern Caucasus and northern Africa) and polyyclic with female diapause (II—France).

14. *Culiseta (Culicella) inconspicua* Lee (1937)

Theobaldia inconspicua: Lee, 1937: 294; Dobrotworsky, 1954: 75. *Culiseta inconspicua* Lee: Stone, Knight and Starcke, 1959: 220; Maslov, 1963: 784, 1964a: 212.

Adult mosquito. The length of the wing is 4.5–6.0 mm and that of the proboscis 3.0–3.4 mm. The palps of the males are relatively short, the same length as the proboscis. Scutellum with 5–6 long marginal setae on each lobe. Spiracular setae only 2. Anterior pronotal lobe without scales and setae. Tarsi uniformly dark, without rings. Abdominal tergites uniformly dark. Hypopygium shown in Fig. 77, a. On each lobe of the 9th tergite, 7–10 setae present. Lateral lobes of gonofurca not large, not reaching one-half the length of the gonocoxite; only long thin setae, without strong setae, present at its apex.

- 152 *Fourth instar larva* (Fig. 77, b and c). The main setae on the head are indistinctly branched: postclypeal and median frontal setae simple, inner frontal seta with two branches. Siphon slightly enlarged medially. The pecten has 9–10 teeth; of these, the distal 2–3 teeth set further apart from each other than the proximal one. Siphon seta simple. The ventral brush has 12 setae set on the common base and 1–2 anterior to it. Anal gills shorter than the anal saddle.

Pupa. Along the posterior margin of the paddle, sharp denticles distinct; much smaller denticles (microtrichia) form a few concentric rows parallel to the rear margin of the paddle.

Distribution (Fig. 75). Australia (Victoria, New South Wales, Tasmania).

Biology. These are predominantly forest mosquitoes found in the hills and plains. Not recorded from human habitations. Attack wild mammals; stray instances of blood-sucking of humans reported. The preimaginal stages occur in small open, unshaded,

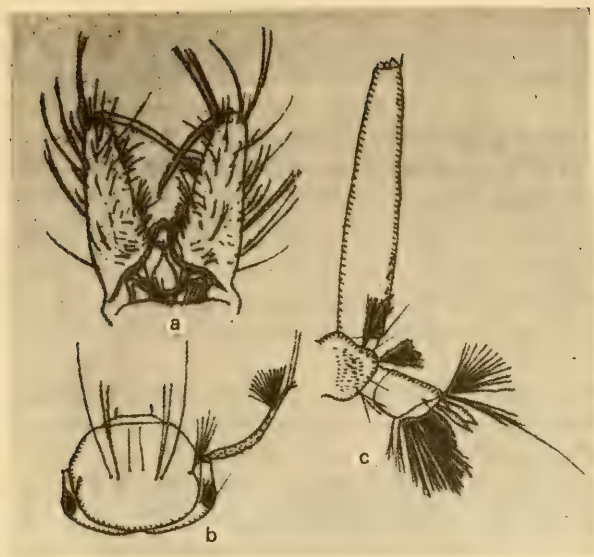


Fig. 77. *Culiseta inconspicua*.

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva (after Lee, 1937).

forest pools with a moderate hypothermal range; are not strangers to isothermal pools. Polycyclic mosquitoes growing without the obligatory diapause (life form VIII).

15. *Culiseta (Culicella) litorea* Shute (1928)

Culicella morsitans litorea: Shute, 1928: 186. *Theobaldia litorea* Shute: Marshall and Staley, 1933: 119; Marshall, 1938: 231; Edwards, Oldroyd and Smart, 1939: 18; Monchadskii, 1951: 139; Harant and Rioux, 1954: 57; Senevet and Andarelli, 1956b: 400; 1960: 305; Kramăr, 1958: 132; Rioux, 1958: 208; Doby, Rault and David, 1960: 174. *Culiseta litorea* Shute: Stone, Knight and Starcke, 1959: 720; Maslov, 1963: 784; 1964a: 212.

Adult mosquito. The wing length is 6 mm. The proboscis with fairly significant shades of light scales. The palps of the males longer than the proboscis by less than the length of the last segment (palpal index less than 100%). Tarsi with narrow apical and basal rings, but the latter hardly noticeable or totally absent on the distal 2-3 segments of the hindtarsi. On the light abdominal sternites, a dark pattern is often seen in the form of the letter V with the pointed end turned anteriorly (Fig. 21, 20). The gonocoxite of the hypopy-

gium not long (index not exceeding 2.5). On each lateral lobe of the gonofurca, 2 (very rarely 3) strong setae. The base of the gonotelopod distinctly enlarged. Tenth sternite with 3 (more rarely 2) apical teeth.

Fourth instar larva. The median and inner frontal setae each consist of 2–3 branches; outer frontal setae with 6–10 branches. The comb has over 120 scales. Siphon seta with 6–8 branches, their maximum length distinctly more than one-third the length of the siphon (40–48%). On the siphon 10–13 teeth are set at equal distances from each other with the exception of the first 1–2 distal ones, which are set widely apart and reach one-third the length of the siphon from its base.

Distribution (Fig. 75). England, Czechoslovakia, Spain, France and islands of the Mediterranean Sea; northern Africa (Algeria). Not reported from the USSR.

Biology. These are mosquitoes of the forest-free plains and marine coasts. Not found near human habitations. Attack wild mammals; blood-sucking of humans and birds not reported. The preimaginal stages develop in open, unshaded, oligo- and β -mesosaprobic sources, not rare in saline waters (up to 3.6 per thousand). Monocyclic with larval diapause.

16. *Culiseta (Culicella) morsitans* Theobald (1901)*

Culex morsitans: Theobald, 1901: 8.

- 153 *Adult mosquito.* The length of the wing is 4.5–7.7 mm and of the proboscis 2.5–3.5 mm. The proboscis and the palps of the females uniformly dark or with scattered areas of light scales. In males, the palps are longer than the proboscis by more than the length of the last segment (palpal index over 100%); the distal two segments of the palps distinctly thickened (Fig. 9, C). Spiracular setae numerous, usually not less than 10 (7–13); similarly, the lower sternopleural (5–15) preepimeral setae not less than 6 (6–12). Anterior femora and tibiae (Fig. 17, 7) anteriorly dark; median and posterior region with fairly significant patches of light scales, sometimes forming a longitudinal light zone on the tibiae. Tarsi with apical-basal narrow rings on the segments, usually absent on the two distal segments on all legs. Abdominal tergite with light basal bands; the dark pattern on the sternites in the form of an upturned letter V absent. Hypopygium shown in Fig. 78, a. Lobe of the 8th tergite with 3–10 spines. On each lateral lobe of the gonofurca, 3–6 strong setae. Gonocoxite relatively long with an index about or slight exceeding 2.5. The base

*Synonyms and sources of literature have been given below while describing the diagnostic features of the subspecies.

154 of gonotelopod not swollen, but uniformly enlarged. Phallus uniformly weakly sclerotized with a pointed distal margin.

Fourth instar larva (Fig. 78, b and c). Branching of the main setae on the head highly variable. All the pecten teeth on the siphon (7-16) set at equal distances from each other and the pecten as a whole usually does not descend beyond one-quarter of the length of the siphon from its base. Setae on the ventral brush anterior to the common base (number 5-9) do not differ distinctly in length from those next to them set on the common base; the length of the latter gradually increases outward. In the pupae, the posterior margin on the paddle usually without teeth (Fig. 56, 2, and 3).

16a. *Culiseta morsitans morsitans* Theobald (1901)

Culex morsitans: Theobald, 1901: 8. *Culiseta morsitans morsitans* Theo.: Maslov, 1963: 787, 1964a: 212. *Theobaldia morsitans* Theo.: Goetghebuer, 1910: 83, 410; Edwards, 1921a: 259; Wesenberg-Lund, 1920-1921: 120; Shute, 1928: 186; Martini, 1929-1931: 217;

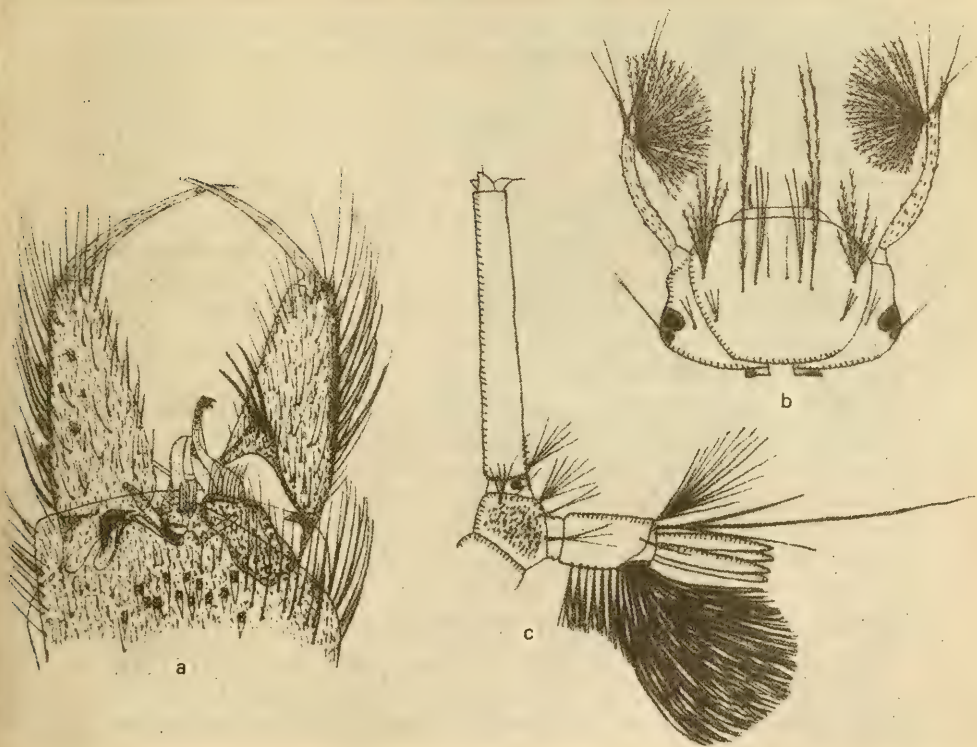


Fig. 78. *Culiseta morsitans*.

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

Monchadskii, 1930: 588, 1936: 211, 1951: 136; Shtakel'berg, 1937: 105; Marshall and Staley, 1933: 119; Marshall, 1938: 227, Edwards, Oldroyd and Smart, 1939: 18; Natvig, 1948: 172; Mihályi, Soós, Sztankay-Gulyás and Zoltai, 1956; Kramář, 1958: 132; Rioux, 1958: 209; Ruffie, 1958: 198; Senevet and Andarelli, 1959a: 293; Sicart and Ruffie, 1960: 643. *Culicada morsitans* Theo.: Theobald, 1910: 302. *Culex calcitrans*: Robineau-Desvoidy, 1827: 409 (partly). *Culex flavivirostris*: Meigen, 1830: 242; Stone and others, 1959: 222. *Culex serratus*: Theobald, 1901: 45 (partly).

Adult mosquito. The legs are relatively very long: femora usually longer than the proboscis. In the 4th-instar larvae, the median frontal setal index (ratio of its length to that of the head) usually 100% (90–120); its branching 1–4 (average 2). Inner frontal seta relatively weakly branched (2–4, more often 3). The comb has usually no less than 125 scales (110–160). Seta 7 posterior to the comb usually simple, very rarely with two branches. Siphon seta usually with more than 5 branches (3–9, average 6).

Distribution (Fig. 75). In the USSR: northwestern, western and central regions of the European part of the USSR, Ukraine, Crimea, Caucasus, central Ural region, southwestern Siberia and Central Asia. Everywhere in Europe; northern Africa (Morocco and Algeria); Asia Minor.

Biology. These are mostly forest mosquitoes migrating to the plains. Very rare in human habitations. The main victims of their attack are birds; very rarely attack man. The preimaginal stages are eurytopic, more often in β -mesosaprobic, moderately hypothermal unshaded pools; found in saline waters, with salinity up to 2.7 per thousand. Usually monocyclic, with larval diapause; another life form, polycyclic with egg diapause has also been reported.

16b. *Culiseta morsitans dyari* Coquillett (1902)

Culex dyari: Coquillett, 1902: 192; Theobald, 1910: 362; Howard, Dyar and Knab, 1915: 457. *Culiseta dyari* Coq.: Dyar, 1928: 243. Theobald, 1907: 412; *Culiseta morsitans dyari* Coq.: Maslov, 1963: 788; 1964a: 212. *Theobaldia morsitans*: Theobald, 1901: 8; Matheson, 1929: 180; Headlee, 1945: 174. *Culiseta (Culiseta) morsitans* Theo.: Matheson, 1944: 224. *Culiseta (Culicella) morsitans* Theo.: Rempel, 1953: 453; Carpenter and La Casse, 1955: 93; Wallis, 1957: 199; Barr, 1959: 52; Stone, Knight and Starcke, 1959: 281; Gjullin, Sailer, Stone and Travis, 1961: 76; Price, 1961: 22; Sommerman, 1964. *Culex brittoni*: Felt, 1905: 79. *Culicella parodites*: Dyar, 1928: 244. *Culiseta (Culicella) parodites* Dyar: Stone, Knight and Starcke, 1959: 221.

155 *Adult mosquito.* The legs are relatively very short: the femora usually shorter than the proboscis.

Fourth instar larva. The index of the median frontal seta (which invariably has two branches) is always over 120% (120–170, average 144%). Inner frontal seta with many branches (3–8, average 4). The comb has usually not more than 115 scales (100–130, average 111); seta 7 posterior to the comb invariably with two branches. Siphon seta more often with 5 branches (4–7).

Distribution (Fig. 75). Canada and USA (Alaska, Colorado, Illinois, Indiana, Ohio and Kentucky).

Biology. These are mostly forest mosquitoes found in the hills and plains. Not reported from human habitations. The main victims of their attack are birds; do not attack man (only stray instances of blood-sucking reported). The preimaginal stages fairly eurytopic; more often develop in β -mesosaprobic, open, unshaded water pools with a moderate hypothermal range. Monocyclic or polycyclic with larval diapause.

17. *Culiseta (Culicella) nipponica* La Casse and Yamaguti (1950)

Theobaldia nipponica: La Casse and Yamaguti, 1950: 84.

Culiseta (Culicella) nipponica La Casse and Yamaguti: Stone, Knight and Starcke, 1959: 221, Maslov, 1963: 789, 1964a: 212.

Adult mosquito. Not known*.

156 *Fourth instar larva* (Fig. 79, a and b). Inner and other frontal setae with many branches; median simple or with two branches. The antennal tuft has 30 or more setal branches. The comb usually bears about 100 (80–120) scales. The extreme upper and median seta (6 or 9) posterior to the comb with identical branching (6–8); extreme lower one has the least number of branches (4–6). The siphon bears 6–10 pecten teeth; of these, one distal tooth is set off from the rest. Siphon seta with 5–9 branches. No less than 14 (14–18) setae on the ventral brush set on the common base and 6 setae anterior to it; the latter do not differ sharply in length from the proximal seta set on the common base.

Distribution (Fig. 69). Japan and Korean peninsula.

Biology. Not known.

*Subsequently, the adult male and female were described in detail by Tanaka et al., 1979: 101–102. See: Tanaka, K., K. Mizusawa and E.S. Saugstad. 1979. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Contrib. Am. Entom. Inst. (Ann Arbor): 16: 1–987. [Editor].

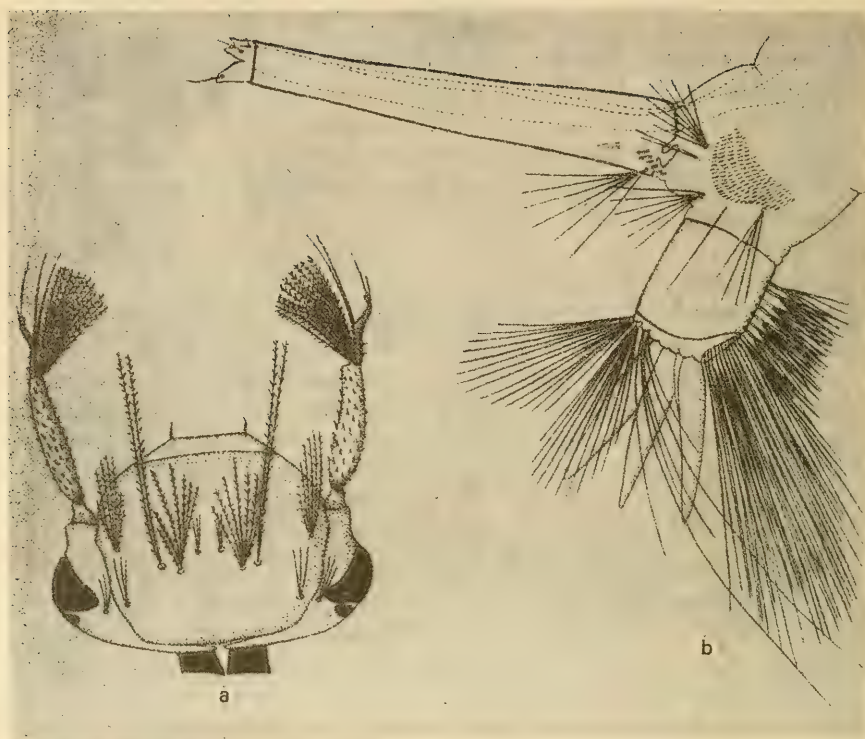


Fig. 79. *Culiseta nipponica* (after La Casse and Yamaguti, 1950).

a—head; b—terminal end of the body of the 4th-instar larva.

18. *Culiseta (Culicella) setivalva* Maslov (1937).

Theobaldia setivalva Masl.: Maslov (cited after Shtakel'berg, 1937: 110); Monchadskii, 1936: 211; 1951: 135; Velichkevich, 1936: 137. *Culiseta setivalva* Masl.: Maslov, 1963: 789, 1964a: 212. *Culiseta setivalva* Montsch.: Stone, Knight and Starcke, 1959: 221. *Theobaldia fumipennis* Steph.: Velichkevich, 1931: 319. *Theobaldia* sp. (Medjid): Martini, 1929–1931: 217.

Adult mosquito. The length of the wing is 5.0–6.9 mm and that of the proboscis 2.8–4.2 mm. The proboscis and the palps of the females dark with scattered distribution of light scales. The palps of the males relatively short, index 1.1–1.35 (average 1.16); palpal index as a rule does not reach 100% (85–105, average 91). Spiracular setae usually less than 10 (6–10, average 8) and the lower sternopleural setae invariably more than 10 (11–14, average 13). The mid- and hindfemora anteriorly placed with a fairly distinct longitudinal

band of light scales. On the distal tarsi, rings are well developed at the base of all the segments; on the fore- and midlegs, the distal tarsal segments often without light rings. Abdominal tergites with distinct light basal bands; some distribution of light scales are common on the distal half of each tergite. On the light sterna we usually see a pattern of dark scales in the form of the letter V with the pointed end turned anteriorly (Fig. 21, 20). Hypopygium shown in Fig. 80. On the 8th tergite (in which the backward extended lobe with the short spines is absent) and on the gonocoxite, some setae bear the typical form of straight nail-like spines. Two more similar spines seen at the apex of the lateral lobe of the gonofurca.

Fourth instar larva. This has relatively indistinctly branched inner frontal setae (not more than 5 branches); median frontal setae usually with not less than two branches (2-4). The comb has more than 120 scales. Median seta posterior to the comb (9) is shorter than the saddle. Distal teeth of the pecten set very widely apart and descend without a specific order beyond the center of the siphon almost to its distal one-third. Seta 5 at the base of the lateral valve of the
157 stigmal plate flabellate. Setae anterior to the common base of ventral

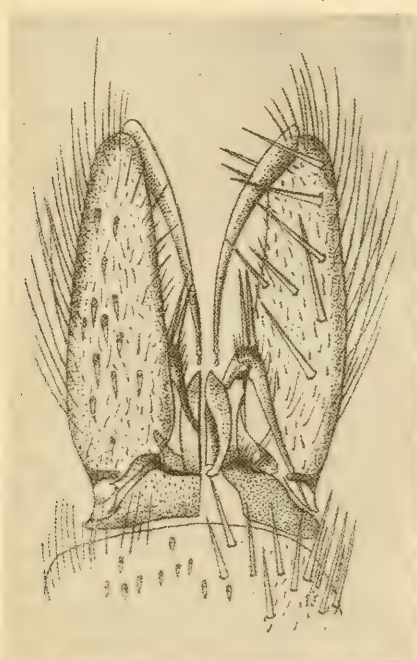


Fig. 80. *Culiseta setivalva*, hypopygium of the male.

brush only slightly shorter or equal in length to the setae next to them on the common base. Outer caudal seta with 3 branches.

Distribution (Fig. 69). Crimea and Asia Minor.

Biology. These are predominantly forest mosquitoes rarely found in the plains. Not found near human habitations, but attacks on man reported from areas near breeding sites. The preimaginal stages live in β - and α -mesosaprobic, open not heavily shaded, isothermal pools. Monocyclic with larval diapause.

19. *Culiseta (Culicella) silvestris* Schingarew (1928)*

Theobaldia silvestris: Shingarev, 1928: 51.

Adult mosquito. The length of the wing is 4.5–7.0 mm and of the proboscis 2.0–4.2 mm. The proboscis and the palps of the females dark with a fairly significant number of scattered light scales. The palps of the males very long (index 1.25–1.65); longer than the proboscis by more than the length of the last segment; palpal index (ratio of the total length of the first four segments to that of the proboscis) in an overwhelming majority of cases exceeds 100% (95–125%). Spiracular setae usually less than 10 (7–10); the number of the lower sternopleural setae is similar (5–10). Tarsal segments with narrow rings, often encircling the apex of the preceding and the base of the subsequent segments; sometimes only the apical rings preserved. Quite often the rings are very weakly manifested and they are often absent on the dorsal surfaces of the tarsi. On the abdominal segments, in most cases, light bands present on the proximal and distal regions of the tergites; sometimes (*C. silvestris amurensis*) the abdominal tergites are entirely dark or have scattered light scales. Spines present on the lobes of the 8th tergite of the hypopygium (*C. silvestris amurensis* and *C. silvestris ochroptera*) or absent (*C. silvestris minnesotae* and *C. silvestris silvestris*). On each lateral lobe of the gonofurca, not less than 3 (usually more) strong setae. The phallus is weakly sclerotized or its apical portion is left intact.

Fourth instar larva. The median frontal seta invariably with two branches. Not less than 100 scales on the comb. The branching of the extreme upper seta (6) posterior to the comb roughly identical with the branching of the extreme lower (13), but weaker than in the median (9). Not more than 13 setae set on the common base of the ventral brush and usually 6–7 lie anterior to it.

*Synonyms and the more important sources of literature have been given below while describing the diagnostic features of the subspecies.

19a. *Culiseta silvestris amurensis* Maslow (1964a: 210)

Theobaldia silvestris amurensis Masl. (without description of the subspecies): Maslov, 1949: 132. *Theobaldia ochroptera*: Peus, 1935: 113; Monchadskii, 1947: 167, 1951: 139; Ch'in and Su, 1959: 197; Ch'in, 1959: 272. *Culiseta ochroptera* Peus: Stone, Knight and Starcke, 1959: 221.

Adult mosquito. The length of the wing is 4.5–7.0 mm and that of the proboscis 2.0–4.2 mm. The overall body color is brown or light brown. Wing spots absent or faintly noticeable (Fig. 4, 1 to 3). Femora and tibiae of all legs very long, noticeably longer than the proboscis; the initial tarsal segments invariably shorter than the proboscis in the fore- and midlegs and invariably longer than the proboscis in the third pair of legs. On the proximal tarsal segments and femora (more rarely on the tibiae), there is usually a longitudinal band of light scales. Extremely narrow, light apical and basal rings in the joints of the proximal tarsal segments of all legs. Abdominal tergites entirely dark or with a few scattered regions of light scales, more rarely with very narrow basal bands of light scales.

A few spines (0–8, average 5) (Fig. 81) are seen on the lobes of the 8th tergite of the hypopygium. On the lobes of the gonofurca, usually not less than 5 strong setae (3–9, average 6). The phallus is relatively weakly sclerotized.

Fourth instar larva. The antennae are slightly bent, moderately long (equal to or slightly shorter than the length of the head). The antennal tuft bears many branches (20–40, average 31). The branching of the outer frontal seta (5–13, average 9) is invariably greater than that of the inner (4–9, average 6). Comparatively few scales (60–100, average 78) in the comb on the 8th segment. The branching of the setae posterior to the comb beginning with the extreme upper one: 4–8 (6); one or two; 5–12 (9); one or two; and 3–7 (5). The siphon is moderately long; index 5–7 (average 6); siphon seta with many branches (5–10, average 7), moderately long. On the pecten, 4–12 (average 8) rather small pecten teeth placed at a distance not further than the proximal one-fourth of the siphon length. Outer caudal seta usually with three branches and inner with many (12–24, average 17). On the common base of the ventral brush, 9–12 (10) setae; anterior to it 6–8 (6–7) setae.

Pupa. The posterior margin of the paddle usually without denticles and pigmented spots (Fig. 56, 1) or with faintly visible (under very high magnifications) rare, extremely tiny setae.

Distribution (Fig. 82). Central Amur regions, Ussuri River basin and southern Primorye; northeastern China.

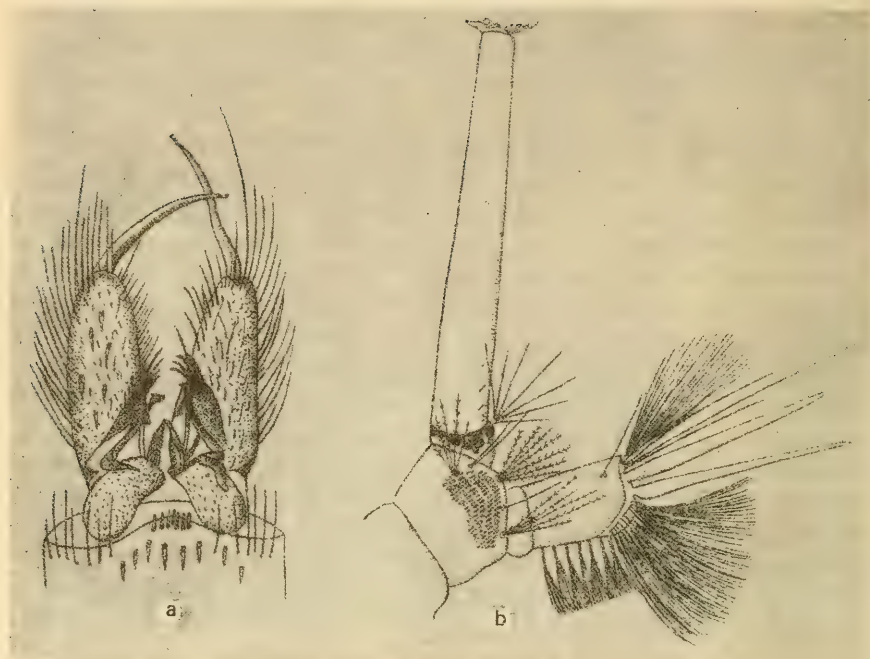


Fig. 81. *Culiseta silvestris amurensis*.

a—hypopygium of the male; b—terminal end of the 4th-instar larva.

159 *Biology.* These are mosquitoes of predominantly forest-free plains; not reported from human habitation. The main victims of their attack are birds, more rarely wild mammals; sometimes attack man near their breeding sites. The preimaginal stages are fairly eurytopic but more confined to the open, rather small, unshaded water pools with isothermal or moderately hypothermal range, oligo-, more rarely β-mesosaprobic water, relatively rich in hydroflora. Polycyclic with larval hibernation; sometimes hibernating females noticed.

19b. *Culiseta silvestris minnesotae* Barr (1957)

Culiseta minnesotae: Barr, 1957: 163, 1959: 52; Price, 1958: 47, 1961: 22; Stone, Knight and Starcke, 1959: 220. *Culiseta silvestris minnesotae* Barr: Maslov, 1963: 795, 1964a: 213. *Theobaldia morsitans* Theo. (partly from the works of American investigators).

Adult mosquito. The length of the wing is 6 mm and of the proboscis 3.2 mm. A distinct admixture of light scales seen on the

wing in the basal half of the costal vein; a spot representing the accumulation of scales at the base of R_{4+5} is distinctly visible. In the proximal articulations of the tarsi (1st-2nd and 2nd-3rd), light apical and basal rings are distinct. On the abdominal tergites proximal and distal bands of light scales present (Fig. 21, 13); 8th tergite entirely light. Hypopygium shown in Fig. 83, a. The phallus in the form of a rectangle with a parallel tube with an intensely sclerotized transverse distal margin.

Fourth instar larva (Fig. 83, b and c). The antennae are usually as long as the head. The antennal tuft is relatively weakly branched (15-20 setal branches). The median frontal setal index is about 150%. The siphon seta has 3-7 branches. The ventral brush bears 11-12 setae set on the common base and 5-7 setae anterior to the common base.

160 *Distribution* (Fig. 82). USA (Minnesota, Wisconsin, Massachusetts, New York, New Jersey, Delaware, Utah, Idaho and Montana).

Biology. These are mosquitoes of the forest-free regions of the hills. Not reported from human habitations; the host not known.



Fig. 82. Range of *Culiseta silvestris amurensis* (1), *C. s. minnesotae* (2), *C. s. ochroptera* (3), *C. s. silvestris* (4), *C. drummondi*, *C. frenchi*, *C. hilli*, *C. otwayensis*, *C. sylvanensis*, *C. victoriensis* (5), *C. weindorferi* (6).

The preimaginal stages found in temporary marshes which do not dry quickly. Polycyclic mosquitoes with female diapause.

19c. *Culiseta silvestris ochroptera* Peus (1935)

Theobaldia ochroptera: Peus, 1935: 113; Monchadskii, 1936: 216, 1951: 139; Shtakel'berg, 1937: 106; Kramář and Minár, 1961: 180. *Culiseta ochroptera* Peus: Stone, Knight and Starcke, 1959: 221. *Culiseta silvestris ochroptera* Peus: Maslov, 1963: 796, 1964a: 213.

Adult mosquito. The costal vein entirely dark. Rings on the tarsi very faintly formed. In males, foretibiae shorter than the proboscis. Proximal and distal light bands present on the abdominal tergites; 8th tergite entirely light. On each lobe of the 8th tergite of the hypopygium, usually 6–8 spines present; on each lobe of the gonofurca 5–8 (more often 6–7) strong setae. The phallus bluntly egg-shaped, uniformly lightly sclerotized all over the surface.

Fourth instar larva. The antennal tuft with many branches (20–37 branched). The siphon seta relatively long, usually not less than one-third of the length of the siphon; consists of 7 branches. In the pecten, 161 7–10 pecten teeth of which 2–3 distal teeth set somewhat more widely apart than the proximal teeth. Seta *f* of the stigmal plate with a sharp bend. The ventral brush bears 12–13 (more often 13) setae set on the common base and 5–8 (more often 6) anterior of the common base.

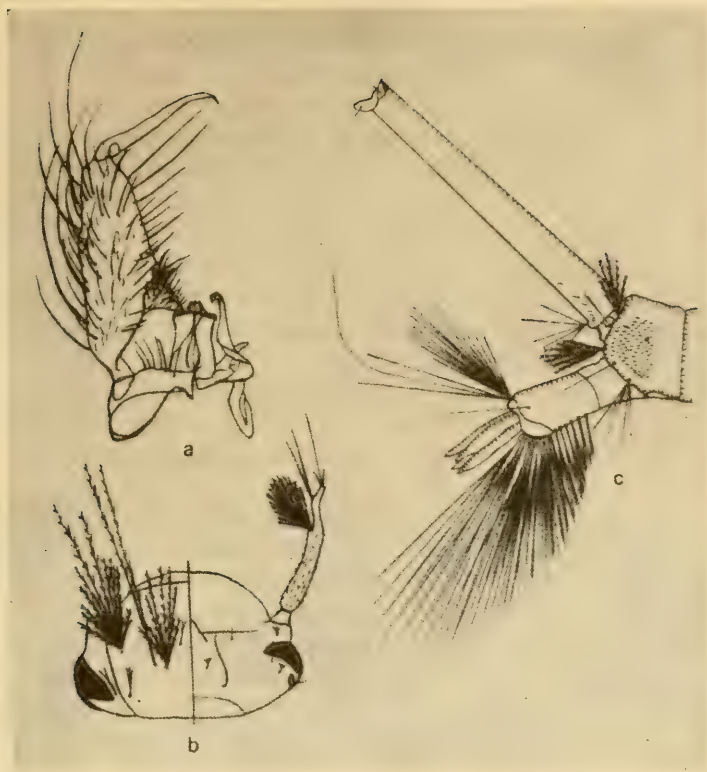
Distribution (Fig. 82). In the USSR, in the northwestern and western European parts. Europe (Czechoslovakia, German Democratic Republic, Federal Republic of Germany).

Biology. These are mosquitoes of the forest-free plains. Not recorded from human habitations and do not attack man. Their hosts are birds and wild mammals. Polycyclic mosquitoes with larval diapause.

19d. *Culiseta silvestris silvestris* Schingarov (1928)

Theobaldia silvestris: Shingarev, 1928: 57. *Culiseta silvestris* Sching. Stone, Knight and Starcke, 1959: 221. *Culiseta silvestris silvestris* Sching. Maslov, 1963: 797; 1964a: 213; *Theobaldia ochroptera* Peus: Shipitsina, 1945: 78 [73]; Popov, 1953: 62.

Adult mosquito. The length of the wing is 5–6 mm and of the proboscis 3–4 mm. The proboscis dark with fairly significant distribution of light scales. In females, all femora and tibiae noticeably longer than the proboscis; the first few segments of the fore- and midtarsi shorter than the proboscis, while those of the hindtarsi longer. In males, the foretibiae are longer than the proboscis. On the wings of the females, there is a distinct spot formed due to accumulation of



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Fig. 83. *Culiseta silvestris minnesotae*.

a—hypopygium of the male (after Barr, 1957); b—head; c—terminal end of the 4th-instar larva (after Price, 1958).

scales at the base. Apical tarsal rings only on the proximal segments. Abdominal tergites with proximal and distal bands articulated with each other through narrow lateral bands of light scales (Fig. 21, 15). Hypopygium shown in Fig. 84. Spines absent on the lobes of the 8th tergite. On each lobe of the 9th tergite, 7–11 setae (average 9). On each lobe of the gonofurca 3–5 (more often 4) slightly bent heavy setae. The form of the phallus approaches a rectangular parallel tubal structure with a heavily sclerotized transverse distal margin.

Fourth instar larva. Antennae shorter than the head; antennal tuft comparatively poorly branched (16–31, average 22 branches). The median frontal seta moderately long; the ratio of its length to that of the head is 115–125% (average 120.5%). The comb usually with not less than 80 scales (65–90, average 75). The median seta posterior

to the comb (9) has 5–8 (average 7) branches. On the common base of the ventral brush, 10–11 (more often 11) setae; 7 setae anterior to the common base.

Distribution (Fig. 82). In the USSR: central regions of the European part, Donets Basin, Ukraine, central Urals and southern regions of western Siberia.

Biology. These mosquitoes are predominantly found in forests of the plains. Not known from human habitations. Their hosts are birds and wild mammals; do not attack man. The preimaginal stages are found in rather small isothermal β -mesosaprobic or oligosaprobic water pools; avoid shaded zones. In the Ukraine, polycyclic with female diapause.

Subgenus *Climacura* Howard, Dyar and Knab (1913)

Climacura: Howard, Dyar and Knab, 1913: 452; Maslov, 1963: 798, 1964a: 213. *Melanoconion*: Theobald, 1903: 238 (partly). *Neomelanoconion*: Theobald, 1907: 514. (?) *Ecculex*: Felt, 1904: 391c (partly). *Mochlostyrax*: Dyar and Knab, 1906: 223 (partly).

Adult mosquito. These are usually dark, at least the tergites, without an admixture of light scales. Anterior pronotal lobe devoid

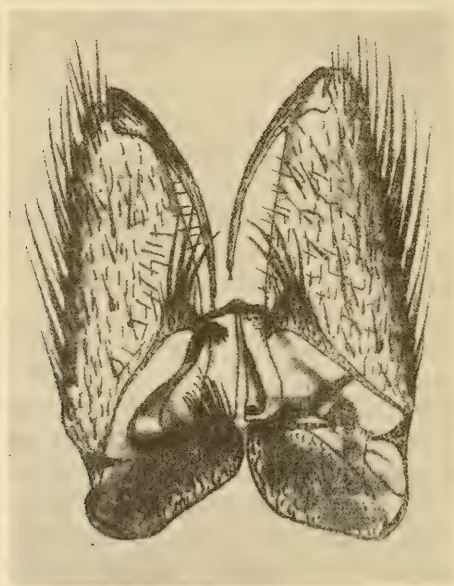


Fig. 84. *Culiseta silvestris silvestris*, hypopygium of the male.

of scales and setae. Spiracular setae and remigium reduced. Legs without light rings near the articulation point. The wing crossvein index positive but, unlike subgenus *Culicella*, does not usually reach 2.0. Hypopygium, as in subgenus *Culicella*, with a weakly sclerotized egg-shaped phallus (Fig. 74, b).

Fourth instar larva. The head is broad with long antennae, flagellate, multiple-branched, antennal seta, filter type mouth parts and many other features as in the members of the subgenus *Culicella*, sharply differing in a medial row of short setae on the siphon apart from the proximal pair of siphon setae. This row extends almost to the very apex of the siphon. The comb of the 8th segment consists of a few scales placed in one transverse row. Anterior to the common base of the ventral brush, only 1-2 setae; if more they are very small and unbranched.

20. *Culiseta (Climacura) antipodea* Dobrotworsky (1962: 291)

Adult mosquito. Small black mosquitoes: the length of the wing is 2.7-3.7 mm and of the proboscis 2 mm. The palps of the males equal to the length of the proboscis and of uniform thickness. One to three spiracular setae and as many lower mesepimeral setae. Tarsi covered with black scales without rings. Tergites and sternites with black scales; only on the 8th sternite are the scales lighter in color. Hypopygium shown in Fig. 85, a. The lobes of the gonofurca are small, 1/5 the length of the gonocoxite, with 2-3 long, stiff setae.

Fourth instar larva (Fig. 85, b and c): Color brown, outer frontal seta with 6-8 branches, median with a single branch and inner with 4-5 branches. Antennae flexed, long, of same length as the head. Antennal tuft with many branches; roughly 30 branches. Premen-tum (Fig. 44, 9) with a broad central tooth and 6-7 lateral teeth on each side. The comb of the 8th segment consists of 14-21 scales, arranged in a single row. Setal branching posterior to the comb beginning from the extreme upper one: 5-9; 1; 6-9; 1; 4-5. Siphon long with an index of 6.1 to 7.5 (average 7). The crest bears 6-9 simple pecten spines. The proximal siphon seta small, with 3-5 branches. Along the siphon 7-8 minute lateral setae; apart from them, there are 2 ventrolateral rows each with 10-12 small setae between the pecten spines and one ventral median row of 5-6 setae with one or two branches on the distal half of the siphon. The lateral seta of the saddle is small, with 3-4 branches. The ventral brush has 11-12 setae on the common base and 2-3 small setae anterior to the common base.

Pupa. Paddle margin without teeth and pigmented spots.

Distribution (Fig. 87). Australia (Victoria and Queensland).

Biology. Larvae in semistagnant small pools and bogs with abundant aquatic vegetation. The biology of the adult mosquitoes is not known (imagoes reared from the eggs, larvae and pupae).

163 21. *Culiseta (Climacura) melanura* Coquillett (1902)

Culex melanurus: Coquillett, 1902: 193; Howard, Dyar and Knab, 1915: 453. *Culicella melanura* Coq.: Theobald, 1907: 6; Dyar, 1928: 243. *Theobaldia melanura* Coq.: Matheson, 1929: 179. *Culiseta melanura* Coq.: Matheson, 1944: 223; Wallis, 1954a: 33; 1959: 157; Carpenter and La Casse, 1955: 95; Burbutis and Lake, 1956: 155; Burbutis and Jobbins, 1957: 68; Hayes, 1958: 70, 1961: 179, 1962: 352; Kissling, 1958: 320; Bjornson, 1961: 19; Siverly and Schoof, 1962: 274; Schober, 1964: 67. Maslov, 1963: 799, 1964a: 218*; *Melanoconion melanura* Coq.: Theobald, 1907: 510, 1910: 457. *Culiseta melanura* Coq.: Ortiz, 1960: 62. *Neomelanoconion indecorabile*: Peryassu, 1908.

Adult mosquito. The length of the wing is 3.2–4.5 mm and of the proboscis 2.5–3.00 mm. Black mosquitoes without light bands, rings or scattered light scales on the proboscis, palps, legs and abdominal tergites. The palps of the males not thickened distally, very long, usually 1.5 times longer than the proboscis; palpal index 110–125% (average 113.8%). Spiracular setae few, not more than 4. Hypopygium shown in Fig. 86, a. The distal margin of the 8th tergite without lobes and without strong spines. On the lateral lobe of the gonofurca, 4–5 stiff setae. The medioapical field of the gonocoxite without lobes or concentrations of setae.

Fourth instar larva (Fig. 86, b and c). Apart from the subgeneric features, these have the following features. The antennae are almost straight and of the same length as the head. The antennal tuft with many branches, flagellate. Outer frontal seta with many branches; median frontal seta simple and long (slightly longer than the head); inner frontal seta without pubescence and a comparatively smaller number of branches, postclypeal seta short and simple. The comb with about 25 scales has an extended base and a rounded distal margin with tiny crenations (Fig. 54). Siphon seta very small with 2–3 branches; in addition to it and the median row of setae, there are 5–6 minute setae with two branches (more rarely with three branches) on the dorsal and ventral surfaces of the siphon. Only 1–2 setae on the ventral brush anterior to the common base.

*See also the editorial article "*Culiseta melanura* . . .". *Pest control*, 1960, 28 (5): 58–60.

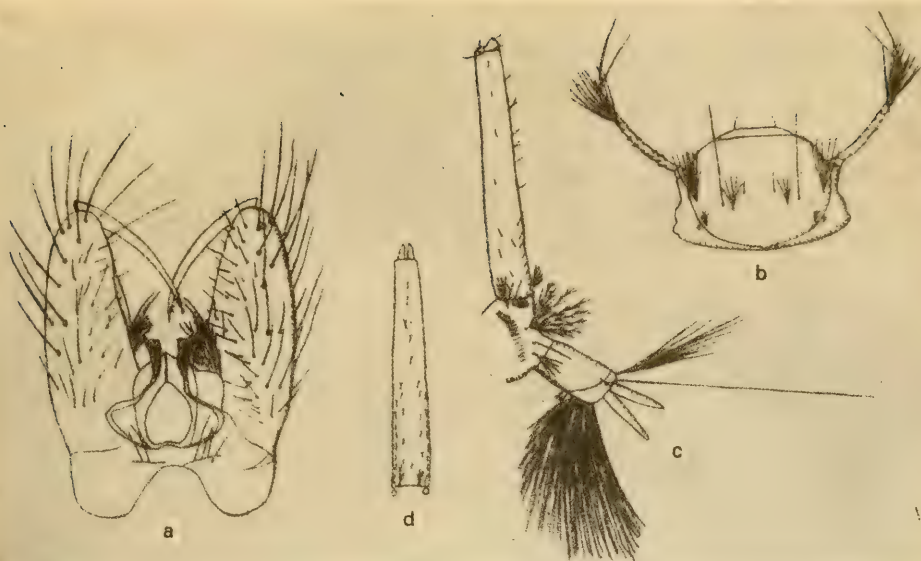


Fig. 85. *Culiseta antipodea* (after Dobrotworsky, 1962).

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva; d—siphon (from below).

Distribution (Fig. 87). USA (everywhere in the southern, central, eastern and northeastern states; in the west and southwest only in Colorado and Washington; in the north, in Iowa, Wisconsin, Michigan and Nebraska) and Mexico (Baja California peninsula).

Biology. These are predominantly forest mosquitoes of the plains. Not known from human habitations. Attack mainly birds, more rarely wild mammals and from time to time humans living close to the breeding sites. These mosquitoes have been reported as the main vectors of eastern equine encephalomyelitis (EEE) and responsible for the spreading of this virus in nature (among birds), as additional vectors of western equine encephalomyelitis (WEE) and possibly of St. Louis encephalitis (SLE). The preimaginal stages are eurytopic but prefer isothermal (in the north) and moderately hypothermal range (in the south) water pools without dense shading and with β -mesosaprobic water. Life forms are diverse: in the north, the mosquitoes are polycyclic with female diapause (II); in the south, polycyclic without essential diapause (VIII). The life form VII, polycyclic with diapause possibly in the larva, pupa and adult stages, has been reported in New Jersey; life form IV, polycyclic with larval diapause, has been reported in Rhode Island.

22. *Culiseta (Climacura) tonnoiri* Edwards, 1925

Theobaldia tonnoiri: Edwards, 1925: 258; Lee, 1937: 294; Miller and Phillipps, 1952: 25. *Theobaldia (Climacura) tonnoiri* Edw.: Edwards, 1932a: 106. *Culiseta (Culiseta) tonnoiri* Edw.: Stone, Knight and Starcke, 1959: 220. *Culiseta (Climacura) tonnoiri* Edw.: Stone, 1961: 44; Belkin, 1962: 284; Dumbleton, 1965: 137. *Theobaldinella tonnoiri* Edw.: Ross, Austin, Miles and Maguire, 1963: 20.



Fig. 86. *Culiseta melaniura* (after Carpenter and La Casse, 1955).

a—hypopygium of the male (original size); b—head; c—terminal end of the 4th-instar larva.



Fig. 87. Range of *Culiseta antipodea* (1), *C. melanura* (2), *C. tonnoiri* (3), *Austrotheobaldia littleri* (4), *Theomyia fraseri* (5), *Allotheobaldia longiareolata* (6).

Female. The length of the wing is 4.5–5.0 mm and of the proboscis 3.0–3.2 mm. The proboscis is entirely with dark scales and the palps covered with dark scales with a small admixture of scattered light scales. Three to five thin spiracular setae, few sternopleural setae and one strong lower mesepimeral seta. Legs with all dark scales, but with subapical light-colored rings on the femora. Wings with distinct spots in the form of accumulations of scales at the bases of R_2 and M_2 , on the distal half of R_5 and in the corresponding section on M . The abdominal tergites and sternites with dark scales, but scales absent at the bases of most tergites, giving the impression of light bands. The first tergite completely without scales. The male has been described by Dumbleton but we have not been able to procure his research paper (1965).

Fourth instar larva (Fig. 88). The head very faintly pigmented. Inner frontal setae branched, of the same length as the head and roughly one-half the length of the median frontal seta with distinct basal pubescence. The comb on the 8th segment consists of 18–20 scales in a single row. Siphon index is 6.5–7.0. The pecten contains

8–10 pecten teeth. Siphon seta is very small, with 3–4 branches. On the siphon, additionally, there are 4 ventral, extremely thin setae with 1–2 branches and 6–8 similarly extremely thin subdorsal (on each side) setae with 1–2 branches. The seta on the saddle small, with 3 branches. The ventral brush has long setae with 12 branches on the common base and 3–4 extremely small setae with 1–2 branches anterior to the common base.

Distribution. New Zealand (Fig. 87).

Biology. The larvae are found (Miller and Phillipps, 1952) in stagnant pools and river backwaters with a rich bottom cover of decomposing organic residue. The larva grows only in the summer. In 1959 and 1960 three virus strains were isolated from the mosquitoes of this species on the hilly forests; one of them (M-78) is geneti-

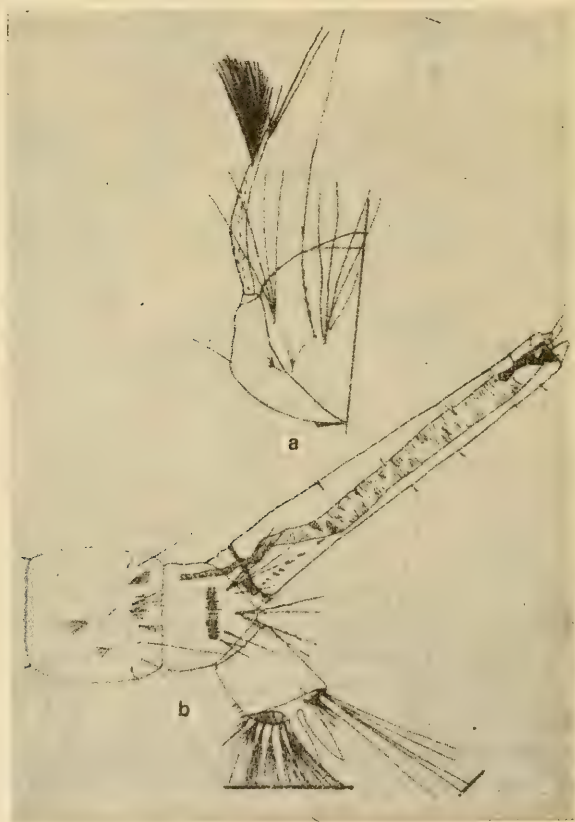


Fig. 88. *Culiseta tonnori* (after Belkin, 1962).

a—head and b—terminal end of the 4th-instar larva.

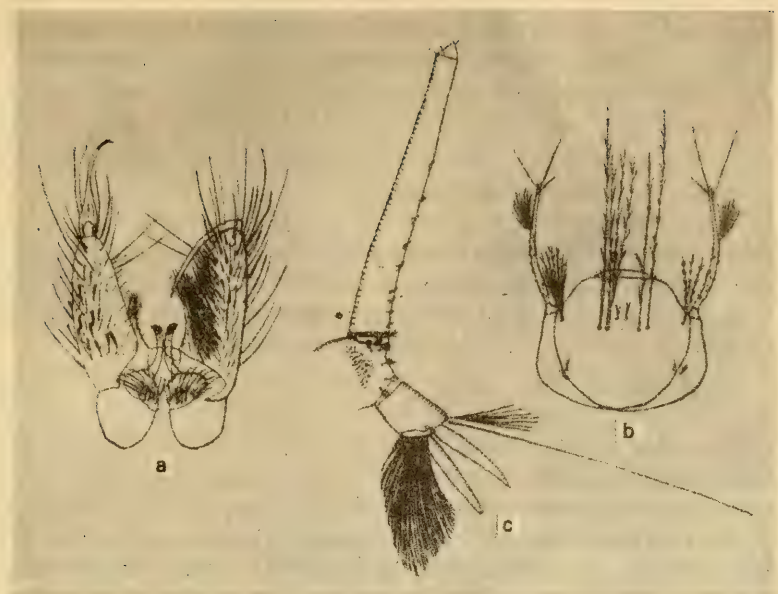


Fig. 89. *Culiseta drummondi* (after Dobrotworsky, 1960).

a—hypopygium of male; b—head; c—terminal end of 4th-instar larva.

cally related to Sindbis virus (MKM-39) and the virus of western encephalitis (WEE) (Ross and others, 1963).

Subgenus *Neotheobaldia* Dobrotworsky (1954)

Theobaldia (subgenus *Neotheobaldia* nov.): Dobrotworsky, 1954: 68. *Culiseta* (*Neotheobaldia*) Dobrotw.: Stone, Knight and Starcke, 1959: 222; Maslov, 1963: 801; 1964a: 213.

Adult mosquito. In these, as in the subgenus *Climacura*, spiracular setae are reduced; there are not more than 4, usually 2–3. On the tarsi, the rings are usually absent or very weakly developed, but quite often the distal 2–3 tarsal segments wholly light in color. Index of transverse wing venation is usually within the range of +1.0 to +1.5. The hypopygium has very large lateral lobes of the gonofurca descending beyond the center of the gonocoxite, usually reaching $\frac{2}{3}$ of its length; most of its basal portion is fused with the gonocoxite. The apex of the lateral lobe is covered by short and long setae without prominent, heavy setae.

Fourth instar larva. The head large and broad. Antennae long, usually not shorter than the head; terminal setae and appendages cover the entire upper portion. The pair of siphon setae located

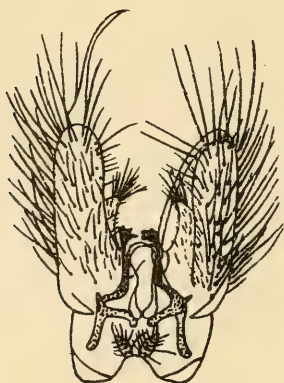
proximally, reduced; they are simple or with two branches or even in the form of an extremely tiny flabellum with many branches. The siphon crest has setae or smooth pecten teeth. Setae absent anterior to the common base of the ventral brush. In the pupa, the posterior margin of the paddle without crenations or these are very faint. The subgenus is endemic for Notogaea.

23. *Culiseta (Neotheobaldia) drummondi* Dobrotworsky (1960)

Theobaldia (Culicella) drummondi: Dobrotworsky, 1960: 241. *Culiseta (Culicella) drummondi* Dobrotw.: Stone, 1961: 44; *Culiseta (Neotheobaldia) drummondi* Dobrotw.: Maslov, 1963: 801. 1964a: 213.

Adult mosquito. The length of the wing is 4.3–5.3 mm and that of the proboscis 3.5 mm. Proboscis dark. The palps of the males of the same length as the proboscis. Three spiracular setae present. Tarsi with indistinct light rings on the proximal segments. Three distal segments of tarsi on the fore- and midlegs and only 2 segments on the hindlegs wholly light. The abdominal tergites with only dark scales. Hypopygium shown in Fig. 89, a. Each lobe of the 9th tergite with 12–14 long setae. At the apex of the large lateral lobe, a tuft of long setae present. The phallus distally enlarged, with tiny denticles at its apex.

Fourth instar larva (Fig. 89, b and c). The body color is milky-white. Antennal tuft with many branches and with 19–24 branches. Inner frontal seta consists of not more than 3 branches; median frontal seta simple. The comb bears over 100 scales. All setae poste-



168 Fig. 90. *Culiseta frenchi*, hypopygium of the male (after Dobrotworsky, 1954).

rior to the comb identical, small and with many branches; the siphon seta and the lateral seta of the saddle also similar. Siphon long, with an index of 8.1–9.3 (average 8.6). The pecten has 8–11 flat, spine-like pecten teeth. The ventral brush has 13–14 setae on a common base.

Distribution (Fig. 82). Australia (Victoria).

Biology. These are forest mosquitoes in rocky areas. Avidly attack man. The preimaginal stages grow in tiny pits (possibly the abandoned burrows of wombats) up to 100 cm deep with turbid water and a distinct hypothermal range. The pits are covered on top with broken tree branches and shrubs and the water is fully shaded.

24. *Culiseta (Neotheobaldia) frenchi* Theobald (1901)

Culex frenchi: Theobald, 1901: 66. *Theobaldia frenchi* Theo.: Edwards, 1924: 363; Lee, 1937: 294. *Theobaldia (Climacura) frenchi* Theo.: Edwards, 1932a: 106. *Theobaldia (Neotheobaldia) frenchi* Theo.: Dobrotworsky, 1954: 72. *Culiseta (Neotheobaldia) frenchi* Theo.: Stone, Knight and Starcke, 1959: 222; Maslov, 1963: 802, 1964a: 213.

Adult mosquito. The length of the wing is 3.8–5.0 mm and that of the proboscis 3.2–3.6 mm. The palps of the males slightly longer than the proboscis. Not more than two spiracular setae present. On each lobe of the scutellum, eight long marginal setae. Hindfemora entirely dark anteriorly. The abdominal tergites with uniformly black scales; the 8th tergite completely covered with pale golden scales. Hypopygium shown in Fig. 90. On each lobe of the 9th tergite, 9–15 setae. Lateral lobe of the gonofurca as in *Culiseta drummondi*. The phallus slightly enlarged distally.

Fourth instar larva. Body color milky-white. Antennal tuft consists of about 10 setal branches. The branching of the dorsal setae on the head slightly more developed than in *C. hilli* (see below). The comb bears about 90 scales; median seta posterior to the comb (9) with 4–5 branches. Other larval structures as in *C. hilli*.

Distribution (Fig. 82). Australia (Victoria).

Biology. These are forest mosquitoes mainly found in the hills, not recorded from human habitations. Attack wild mammals and occasionally man. The preimaginal phases grow in intensely hypothermal (larvae die at temperatures of about 20°C), α -mesosaprobic subsoil waters (tunnels of land crayfish). Polycyclic, without the essential diapause.

24a. *Culiseta frenchi frenchi* Theobald (1901: 66).

24b. *Culiseta frenchi atritarsalis* Dobrotworsky (1954: 73)

These two subspecies differ in the following way: in the former, the first 3 distal tarsal segments of all legs are completely light while, in the later, the tarsi are entirely dark. The distribution and ecology of these two subspecies are identical.

25. *Culiseta (Neotheobaldia) hilli* Edwards (1926)

Theobaldia hilli: Edwards, 1926b: 111; Lee, 1937: 294. *Theobaldia (Climacura) hilli* Edw.: Edwards, 1932a: 106. *Theobaldia (Neotheobaldia) hilli* Edw.: Dobrotworsky, 1954: 69. *Culiseta (Neotheobaldia) hilli* Edw.: Stone, Knight and Starcke, 1959: 222; Maslov, 1963: 803, 1964a: 213.

Adult mosquito. The length of the wing is 3.5–3.8 mm and of the proboscis 2.3–3.0 mm. Palps of the males slightly shorter than the proboscis. Spiracular setae only two. On the tarsi, the proximal segments are dark, without rings; the two distal tarsal segments of all legs entirely light. On the 5th–7th abdominal tergites we find 169 apical angular spots of light scales (Fig. 21, 16). Hypopygium shown in Fig. 91, a. On each lobe of the 9th tergite, 9–10 setae present. The apex of the lateral lobes of the gonofurca very large, almost reaching the apex of the gonocoxite. The apex of the lobe with a tuft of long thin setae. The phallus is distinctly enlarged distally.

Fourth instar larva (Fig. 91, b and c). Milky-white in color. Antennae roughly of the same length as the head. Antennal tuft with 10 setal branches. The outer frontal seta with many branches (5–8), less distinctly branched than the inner (4–6) and even more indistinct than the median (3–4); all are roughly identical in length, slightly over one-half the length of the head. Postclypeal setae (3–5 branches) small, one-half the length of the frontal setae. The comb has about 90 scales. Marginal upper seta (6) posterior to the comb with 3–4 pubescent branches; median (9) with 3 branches, pubescent; marginal lower one (13) weakly pubescent (2–3 branches). Siphon moderately short with index 5.0 to 5.4. Siphon seta with 2 branches. Along with the pecten teeth, there are 7–11 setae on the siphon crest. Lateral seta of the saddle small with 3–4 branches. The ventral brush has 12–14 setae on a common base. Outer caudal seta, very long, simple.

Distribution (Fig. 82). Australia (Victoria).

Biology. These are forest mosquitoes of the hills, absent in human habitations. The victims of their blood-sucking are wild mammals. Occasionally, they attack man. The preimaginal stages

grow in the very hypothermal α -mesosaprobic subsoil waters (burrows of land crayfish). Polycyclic with larval diapause; possibly, monocyclic with egg diapause.

170 26. *Culiseta (Neotheobaldia) otwayensis* Dobrotworsky (1960)

Theobaldia (Culicella) otwayensis: Dobrotworsky, 1960: 146. *Culiseta (Culicella) otwayensis* Dobrotw.: Stone, 1961: 44. *Culiseta (Neotheobaldia) otwayensis* Dobrotw.: Maslov, 1963: 804, 1964a: 213.

Adult mosquito. The length of the wing is 3.8–4.5 mm. The proboscis of the female is uniformly colored. In males, the palps are shorter than the proboscis. Spiracular setae very weak, numbering 2–5. On the median lobe of the scutellum, 6–8 long marginal setae. Tarsi and abdominal tergites dark without rings and bands. Hypopygium shown in Fig. 92, a. The lobes of the 9th tergite indistinct, bearing 1–2 stiff setae. The large lateral lobes of the gonofurca all

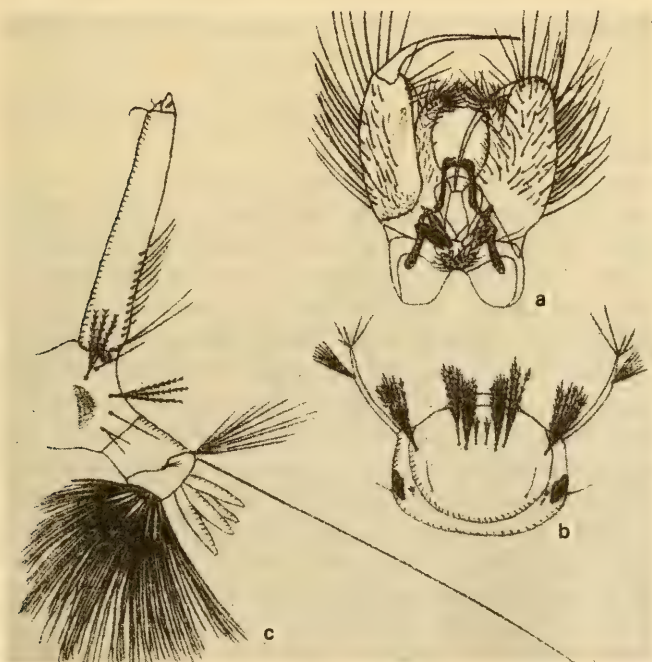


Fig. 91. *Culiseta hilli* (after Dobrotworsky, 1960).

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

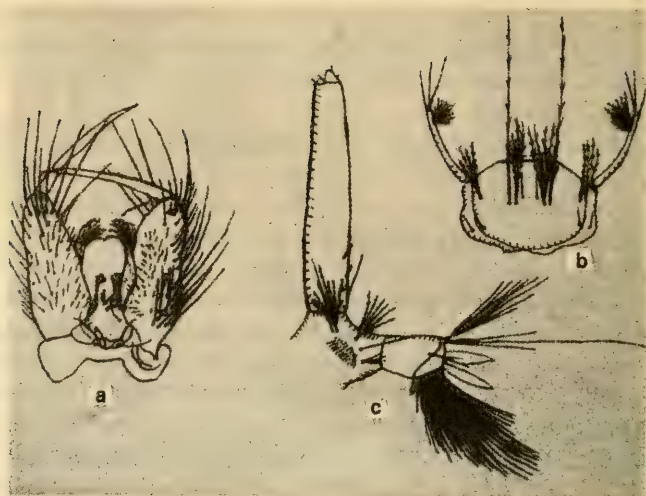


Fig. 92. *Culiseta otwayensis* (after Dobrotworsky 1960).

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

along its length fused with the gonocoxite body. The phallus is ellipsoidal.

Fourth instar larva (Fig. 92, b and c). The body color brownish. Antennae slightly shorter than the head. Antennal tuft weakly developed with 2–5 setal branches*. Inner frontal seta branched similarly (3–5) to the outer (3 to 4); median frontal seta simple, long, over 1.5 times the length of the head. The comb has 50–60 scales. The marginal upper seta (6) posterior to the comb with many branches (8–9), sharply pubescent; median (9) also pubescent, with 5–6 branches, lower marginal (13) short, glabrous, with 3–4 branches. Siphon moderately short (index 4.8–5.6). Pecten weakly developed, with 3–5 crenated pecten teeth or spines. Siphon seta simple. Lateral seta on the saddle small ($1/3$ the length of the saddle), with two branches. Outer caudal seta has a lone central branch, which is very long and two lateral ones which are extremely short. The ventral brush has 14–16 setae on the common base and 1–2 anterior to it.

Distribution (Fig. 82). Australia (Victoria).

171 **Biology.** The preimaginal stages found only once in a pool

*As stated by Dobrotworsky in the text (1960, p. 247), however, it was shown with many branches in the diagram (Fig. 3 on p. 244; here, Fig. 92 b).

under an uprooted tree with a highly shaded water surface and a distinct hydrothermal condition.

27. *Culiseta (Neotheobaldia) sylvanensis* Dobrotworsky (1960)

Theobaldia (Culicella) sylvanensis: Dobrotworsky, 1960: 245. *Culiseta (Culicella) sylvanensis* Dobrotw.: Stone, 1961: 44. *Culiseta (Neotheobaldia) Dobrotw.*: Maslov, 1963: 806, 1964a: 213.

Adult mosquito. The wing length is 3.7–4.3 mm and that of the proboscis 3.2 mm. The palps of the males longer than the proboscis. One or two spiracular setae; on each lobe of the scutellum six to eight long marginal setae. Hindfemora anteriorly pale with a longitudinal black band. Proximal segments of the tarsi without rings; 2–3 distal tarsal segments of all legs all light. Hypopygium shown in Fig. 93, a. On each lobe of the 9th tergite, 8–10 long setae. Lateral lobe of the gonofurca with a tuft of long setae on the apex. The phallus distally slightly enlarged with a few small denticles at the apex.

Fourth instar larva (Fig. 93, b and c). Color milky-white. Antennae shorter than the head. Antennal tuft relatively weakly developed, with 5–10 setal branches; outer frontal seta noticeably shorter than the inner; their branching is identical (4–8 branches); median frontal seta (with 3–5 branches) longest but even it is shorter than

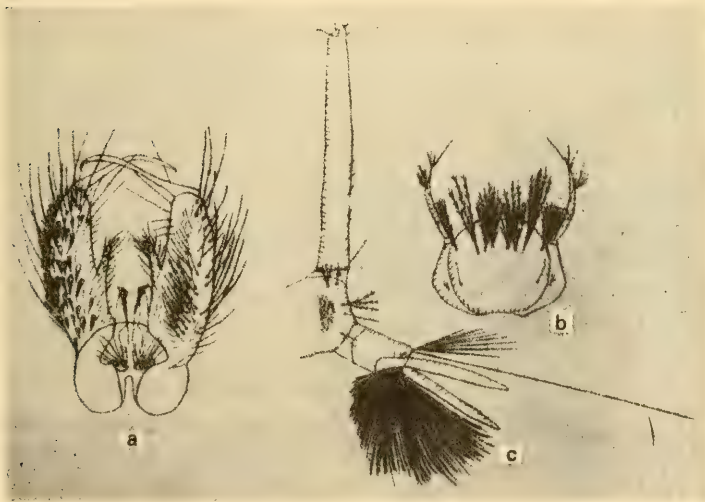


Fig. 93. *Culiseta sylvanensis* (after Dobrotworsky, 1960).

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

the head. The comb has over 100 scales. Branching of the setae posterior to the comb; 2-4; 1; 2-4; 1; 2-3. Siphon long; index 5.5-7.9 (average 6.7). Siphon seta simple, moderately long. The pecten has 8-11 smooth pecten spines, without crenations. Lateral seta of the saddle small, with many branches. Outer caudal seta simple, very long. The ventral brush has 14 setae set on the common base.

Distribution (Fig. 82). Australia (Victoria).

Biology. These mosquitoes are found in the forests of rocky regions. Most frequently attack man. The preimaginal phases are found in
 172 deep (to 100 cm) pits (probably burrows abandoned by wombats) with muddy (α -mesosaprobic) water with sharp hypothermal variations and total shade (pits on top covered by branches of shrubs and broken trees).

28. *Culiseta (Neotheobaldia) victoriensis* Dobrotworsky (1954)

Theobaldia (Culicella) victoriensis: Dobrotworsky 1954: 73. *Culiseta (Culicella) victoriensis* Dobrotw.: Stone, Knight and Starcke, 1959: 221. *Culiseta (Neotheobaldia) victoriensis* Dobrotw.: Maslov, 1963: 807, 1964a: 213.

Adult mosquito. The length of the wing is 4.0-4.7 mm and of the proboscis 3.3-3.6 mm. The palps of the males nearly as long as the proboscis. Spiracular setae 2-3. The proximal segments of the tarsi with basal, light rings; additionally on the third tarsal segment, there is also an apical ring; two distal segments of all tarsi uniformly light. Abdominal tergites uniformly dark, with the exception of the light distal margin of the 8th tergite. Hypopygium shown in Fig. 94, a. On each lobe of the 9th tergite, 10-12 setae. Lateral lobes of the gonofurca large as in *C. sylvanensis*. The phallus distally enlarged, without apical denticles.

Fourth instar larva (Fig. 94, b and c). The body color milky-white. Antennae the same length as or slightly longer than the head. Antennal tuft with 14-16 setal branches. Outer frontal seta relatively short (about one-half the length of the head), with many branches. The inner (4-5 branches) long, of the same length as the head; median with two branches, very long, 1.5 times longer than the head. The external clypeal seta extremely small, simple or with two branches. The comb has less than 100 scales. Branching of the setae posterior to the comb: 4-5; 1; 2-3; 1; 2. The siphon is moderately long with an index of about 6. The pecten has 10-13 spiny pecten teeth; two distal pecten teeth more widely spaced and the pecten generally extends to or slightly beyond the middle of the siphon. The outer caudal seta moderately long, simple. Lateral seta of the

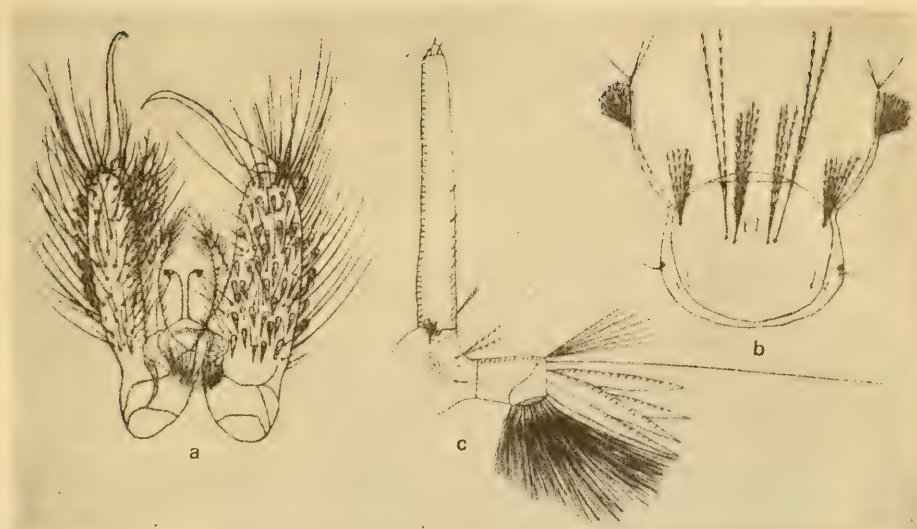


Fig. 94. *Culiseta victoriensis* (after Dobrotworsky, 1960).

a—hypopygium of the male; b—head; c—terminal end of the 4th-instar larva.

saddle small, with 2–5 branches. The ventral brush has 15 setae set on the common base.

173 *Distribution* (Fig. 82). Australia (Victoria).

Biology. These are mosquitoes of forest hilly regions, absent from human habitations. Attack wild mammals; sometimes also man. The preimaginal stages live in subsoil waters (burrows of land crayfish) with distinct hypothermal and α -mesosaprobic water. Polycyclic with larval diapause (monocyclic with egg diapause also possible).

29. *Culiseta* (*Neotheobaldia*) *weindorferi* Edwards (1926)

Theobaldia weindorferi: Edwards, 1926b: 111; Lee, 1937: 296. *Theobaldia* (*Climacura*) *weindorferi* Edw.: Edwards, 1932a: 106; *Culiseta* (*Climacura*) *weindorferi* Edw.: Stone, Knight and Starcke, 1959: 221. *Culiseta* (*Neotheobaldia*) *weindorferi* Edw.: Maslov, 1963: 808, 1964a: 213.

Adult mosquito. The palps of the males as long as the proboscis. The pronotal lobe devoid of setae and scales. On each lateral lobe of the scutellum, 6–9 long marginal setae; on the median lobe 8–10 setae. Tarsi uniformly dark, without rings. Hypopygium shown in Fig. 95. Six setae present on each lobe of the 9th tergite. Lateral lobe

of the gonofurca moderately large, descending with its apex beyond the center but not reaching to $2/3$ of the length of the gonocoxite; the apex of the lobe with long, but not stiff setae. The phallus almost rectangular, weakly sclerotized with a flattened apex. The preimaginal phases not known.

[Fourth instar larva.*]

Distribution (Fig. 82). Australia (Tasmania).

Biology. Not known.

2. Genus *AUSTROTROTHEOBALDIA* Dobrotworsky (1954)

Theobaldia (subgenus *Austrotheobaldia* nov.): Dobrotworsky, 1954: 68. *Culiseta* (*Austrotheobaldia*) Dobrotw.: Stone, Knight and Starcke, 1959: 220. *Austrotheobaldia* Dobrotw. comb. nov. Masl.: Maslov, 1963: 809, 1964a: 213.

Adult mosquito. Spiracular setae numerous, small postspiracular scales also present. The palps of the males shorter than or equal to the length of the proboscis. All tarsal segments uniformly dark. Hypopygium shown in Fig. 96, a. The lobes of the 9th tergite bear long thin setae numbering not less than 4. The large lateral lobes of the gonofurca, including its apex reaches $2/3$ the length of the gonocoxite, the gonofurca is set off from the gonocoxite almost all along its length. The apex of the lobe is densely covered with both fine setae and spiny setae. The phallus oval or ovoid, weakly sclerotized.

Fourth instar larva. All setae are without pubescence. The head (Fig. 96, c) is very large and broad. Antennal tuft weakly branched. Two of the terminal antennal setae placed slightly anterior to the apex. One regular basal row of long scales in the comb and, away from it distally, a spot of long scales. The weak siphon seta placed close to the center of the siphon and not basally (Fig. 96, b). On the ventral brush, only setae set on the common base. Monotypic genus of Notogaea.

1. *Austrotheobaldia littleri* Taylor (1913)

Chrysoconops littleri: Taylor, 1913: 702. *Theobaldia littleri* Tayl.: Edwards, 1924: 363; Lee, 1937: 294. *Theobaldia* (*Climacura*) *littleri* Tayl.: Edwards, 1932a: 106. *Theobaldia* (*Austrotheobaldia*) *littleri* Tayl.: Dobrotworsky, 1954: 75. *Culiseta* (*Austrotheobaldia*)

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*Pupae and larvae of this species were described and illustrated in 1966. See: Dobrotworsky, N.V. 1966. Mosquitoes of Tasmania and Bass Straits Islands. *Proc. Linn. Soc. N.S. Wales*, 91: 121-146 [Editor].

littleri Tayl.: Stone, Knight and Starcke, 1959: 220. *Austrotheobaldia littleri* Dobrotw.: Maslov, 1963: 810, 1964a: 214.

Adult mosquito. The length of the wing is 3.8–4.5 mm and of the proboscis 2.5–2.8 mm. The proboscis and the palps uniformly dark. Three thin spiracular setae. Each lateral lobe of the scutellum has 4–6 and on an average 6–8, long marginal setae. Legs uniformly dark without rings or light scales. Abdominal tergites uniformly dark. On the 8th tergite of the females, the scales are mixed, dark and light (Fig. 21, 4). Hypopygium shown in Fig. 96, a. On each lobe of the 9th tergite, 4–7 (up to 10) setae. Gonocoxites moderately long (index around 3). Heavy spines on the apex of the lateral lobe.

Fourth instar larva (Fig. 96, b and c). Body color rusty brown. Antennae nearly as long as the head. Antennal tuft consists of 7 branches. Setae on the head weakly branched. Outer frontal seta moderately long (slightly shorter than the length of the head), with 2 branches; median frontal—simple, twice as long as the head; inner frontal over 1.5 times the length of the head, with 2–3 branches. Postclypeal seta small, simple. The comb has 16–30 small scales in the basal row and 8–15 long scales gathered in the usual “spot” of scales. Branching of the setae posterior to the comb: 8–9; 1; 3–5; 1; 3. Siphon long (index 7). Siphon seta simple or with two branches. On the pecten, 13–14 small, triangular teeth, not reaching the base of the siphon seta. Lateral seta of the saddle as long as the saddle, simple. Outer caudal seta consists of a single very long branch and two extremely short additional small branches. The ventral brush has only 10–11 setae set on the common base.

Distribution (Fig. 87). Australia (Victoria, New South Wales, Tasmania).

Biology. These are mosquitoes found in hilly forests, absent from human habitation. Attack large mammals and birds; blood-



Fig. 95. *Culiseta weindorferi*, hypopygium of the male (after Lee, 1937).

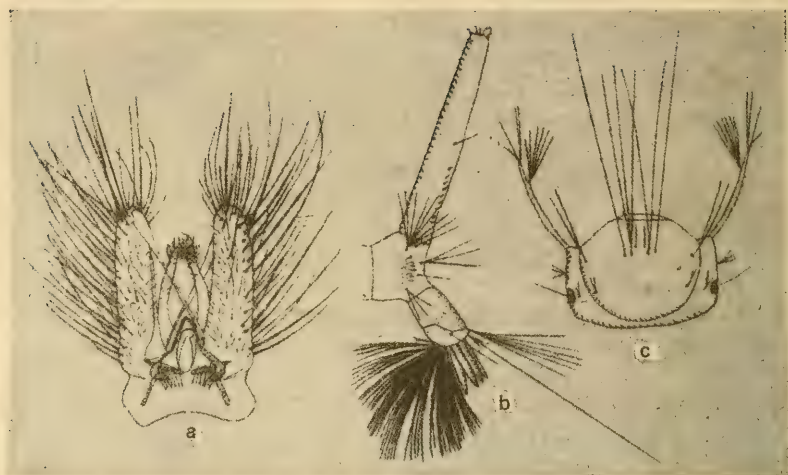


Fig. 96. *Austrotheobaldia littleri* (after Dobrotworsky, 1954).

a—hypopygium of the male; b—terminal end of the 4th-instar larva; c—head.

sucking on man has not been reported. The preimaginal stages live in deep pits (formed by the uprooting of trees) with β - and α -mesosaprobic water in deep shade and with a hypothermal range (larvae perish at temperatures above $+20^{\circ}\text{C}$). Polycyclic with larval diapause (monocyclic with egg diapause also possible).

3. Genus *THEOMYIA* Edwards (1930)

Theobaldia (subgenus *Theomyia* nov.): Edwards, 1930: 303. *Culiseta* (*Theomyia* Edw.): Stone, Knight and Starcke, 1959: 222. *Theomyia* Edw. comb. nov. Masl.: Maslov, 1963; 811, 1964a: 214.

Adult mosquito. The palps of the males very short, about one-half the length of the proboscis, bare. Spiracular setae weakly developed. Subcostal setae absent. Crossveins on the wing (R-M and m-cu) almost fuse with each other (index zero). The main structures of the hypopygium are the same as in mosquitoes of the genus *Culiseta*.

Fourth instar larva. Has a broad head and mouth parts of filtration type, but the antennae short and slightly thickened medially (Fig. 97, a). Antennal tuft with a few branched setae. A pair of large thin walled air sacs present in the thoracic regions. On the thorax and abdomen we find small dendritic setae. Siphon very long, with

index over 7, intensely sclerotized. Pecten with biserrate pecten spines. Siphon seta occupies a proximal position. Outer and inner caudal setae long and simple. The ventral brush has setae set only on the common base. Monotypic genus, endemic for equatorial Africa.

1. *Theomyia fraseri* Edwards (1914)

Leptosomatomyia fraseri: Edwards, 1914: 174[74]. *Theobaldia* (*Theomyia*) *fraseri* Edw.: Edwards, 1930: 303; Haddow, Van Someren, Lumsden, Harper and Gillett, 1951; Van Someren, 1956: 3; Hopkins, 1952: 79. *Culiseta* (*Theomyia*) *fraseri* Edw.: Stone, Knight and Starcke, 1959: 222. *Theomyia fraseri* Edw.: Maslov, 1963: 812, 1964a: 214.

Adult mosquito. Body color reddish brown or yellowish brown; dark scales with a purple shade. Wings with uniform dark scales, without 176 spots. Legs dark with basal, light rings on the two proximal segments of the fore- and midtarsi. Abdominal tergites with lateral longitudinal bands of silvery white scales (Fig. 21, 19). Hypopygium has not been described, but it has been stated that it is simple, nearly the same as in *Culiseta* (Edwards, 1914).

Fourth instar larva (Fig. 97, a and b). The antennal tuft bears roughly 10 highly pubescent branches. Median and inner frontal setae moderately long, both identical, with 2-3 branches. Prementum typical in structure (Fig. 44, 10). On the comb, about 50 scales. Setae posterior to the comb: marginal upper with two branches; median with many branches, pubescent; all others simple. Siphon nearly black with an index of 8. Siphon seta simple. On the pecten, 25 doubled, thin pecten spines. Outer and inner caudal setae simple, long. The ventral brush with 16 setae set on the common base. Dorsal anal gills almost twice as long as the ventral ones.

Distribution (Fig. 87). Africa (from Sierra Leone and Cameroons to Uganda, Kenya, Ethiopia).

Biology. These are mosquitoes of hilly forests, absent from human habitations. Attack mammals and birds and equally feed avidly on humans close to breeding sites. The preimaginal stages live in small water pools formed in tree holes.

4. Genus *ALLOTHEOBALDIA* Brolemann (1919)

Theobaldia (subgenus *Allotheobaldia*): Brolemann, 1919: 90. *Culiseta* (*Allotheobaldia* Brol.): Stone, Knight and Starcke 1959: 221. *Allotheobaldia* Brol. comb. nov. Masl.; Maslov, 1963: 813, 1964a: 214.

Adult mosquito. Head and its appendages, thorax, legs and abdominal tergites covered with broad, dark and white scales, forming a distinct pattern. The palps of the males slightly shorter

than the proboscis, enlarged distally in the form of a spatula; usually, the boundary between the 2nd and 3rd segments distinctly visible. In the females, the 8th sternite with broad, projecting lobes and deep groove between them (Fig. 25). Hypopygium shown in Fig. 23. The 9th tergite is massive, H-shaped, with long clavate processes turned posteriorly. Gonocoxite broad with the lobe extended outward. Gonofurca in the form of two narrow lobes separated from each other; the lobes placed beyond the center of the gonocoxite. Gonotelopod with two fore-apical digitate appendages. The tenth segment is heavily sclerotized with a characteristic, pointed, club-shaped process of the sternite. Gonoepimerite fused with the apodeme of the gonocoxite in the form of a broad semicylindrical plate. The phallus in the form of a pair of plates twisted like a coil.

Fourth instar larva. Short antennae and relatively weak antennal tuft. Siphon relatively short. Index less than 2.5. Saddle incomplete, hiding the anal segment dorso-ventrally (up to one-half of the segment). Outer caudal seta with multiple branches, inner simple or with two branches. The ventral brush bears distinct setae set on the common base and anterior to it. Monotypical Mediterranean genus.

1. *Allotheobaldia longiareolata* Macquart (1838)

Culex longiareolatus: Macquart, 1838: 34; Blanchard, 1905; Theobald, 1901: 342. *Theobaldia longiareolata* Macq.: Langeron, 1918: 98; Brolemann, 1919: 90; Edwards, 1921a: 287; Kirkpatrick, 1925: 75; Martini, 1929-1931: 214; Monchadskii, 1930: 583, 1936: 191, 1951: 118; Petrishcheva, 1936: 49, 1954: 243; Shtakel'berg, 1937: 94;

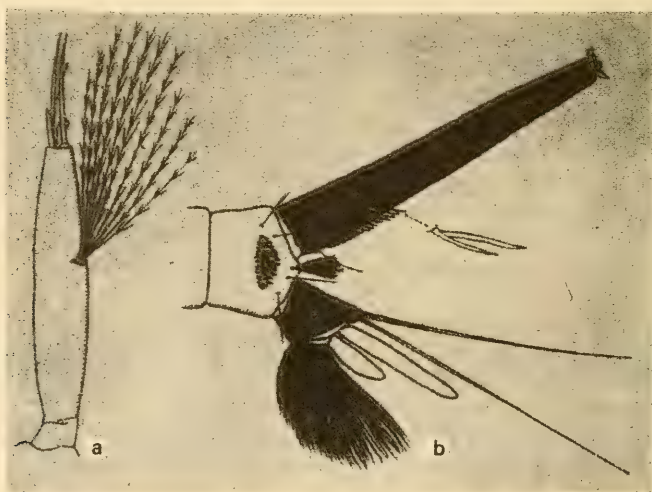


Fig. 97. *Theomyia fraseri* (after Edwards, 1930).
a—antenna; b—terminal end of the 4th-instar larva.

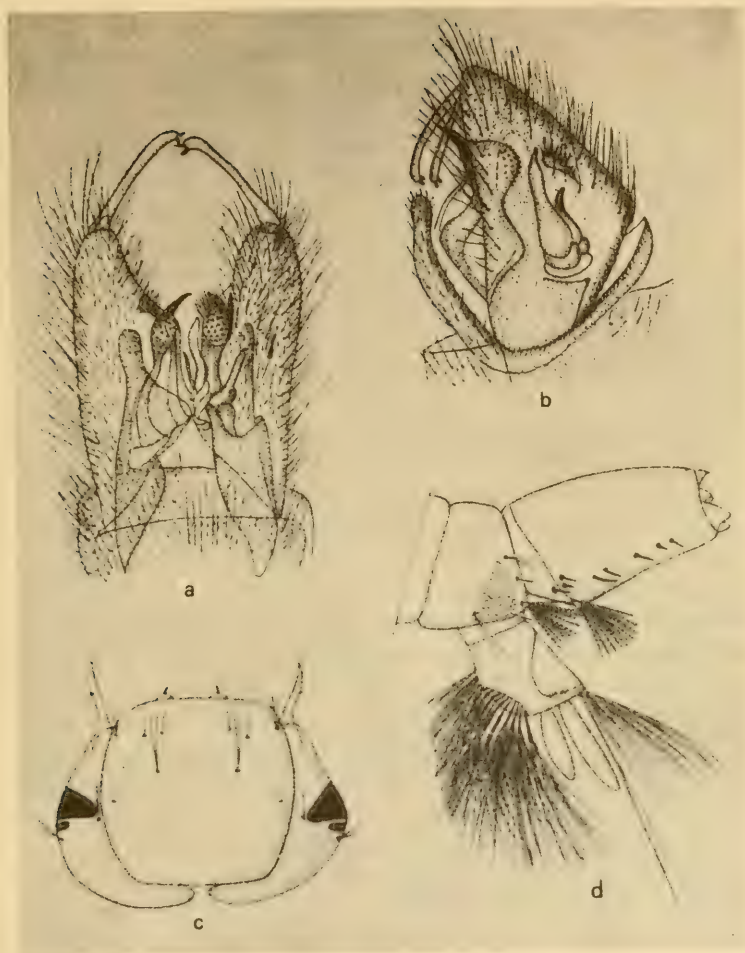


Fig. 98. *Allotheobaldia longiareolata*.

a and b—hypopygium of the male (ventral view and lateral view); c—head;
d—terminal end of the 4th-instar larva.

- Hopkins, 1952: 77; Rioux, 1958: 196; Ruffie, 1958: 192; Senevet and Andarelli, 1959a: 237; Sicart and Ruffie, 1960: 643. *Culiseta* (*Allotheobaldia*) *longiareolata* Macq.: Stone, Knight and Starcke, 1959: 221. *Allotheobaldia longiareolata* Macq.: Maslov, 1952: 69, 1955: 9, 1957b: 14, 1961a: 865, 1963: 814, 1964a: 214. *Culex spathipalpis*: Rondani, 1872: 31, Theobald, 1901: 339. *Theobaldia spathipalpis* Rond.: Theobald, 1903: 154, 1907: 276, 1910: 273. *Culex leucogrammus*: Loew, 1874: 413. *Culex serratipes*: Becker, 1908: 78. *Culex annulatus maroccanus*: d'Anfreville, 1916: 141.

Adult mosquito. The length of the wing is 2.7–7.5 mm and of the proboscis 2.2–5.8 mm. Head on top with broad white scales. Thorax, also similar, with the scales dorsally forming a typical lyrate-shaped pattern (Fig. 11, 21 to 24). All lateral thoracic setae are well developed. Spiracular 5–9 (average 7); lower sternopleural 4–10 (average 8); lower mesepimeral 2–6 (average 4). Wings spotted (Fig. 4, 4 to 6) with fairly significant scattering of light scales (Fig. 3, 4 to 6). On the legs, with the exception of the distal 2–3 tarsal segments (Fig. 17, 8), a distinctly characteristic punctate pattern of prominent spots made up of broad white scales. Abdominal tergites with basal light bands which are uniformly broad or constricted laterally or medially; fairly numerous scattered light scales are common on the dark tergite sections. Hypopygium shown in Figs. 23 and 98, a and b. The 8th tergite without the posteriorly extended median lobe. The 9th tergite with clavate processes sharply extending posteriorly and set with short setaceous hair. Gonocoxite medially broad with a deep groove where a very large phallus and the 10th segment are located. Gonotelopod slightly broadened in the apical portion where two digitate appendages are present (Fig. 24, 7).

Fourth instar larva (Fig. 98, c and d). Color of head very dark, almost black; antennae short, usually not more than one-third the length of the head (20–40, average 31%). Antennal tuft with 2–4 (average 3) setal branches. Setae on the head weakly developed: outer frontal with 2–4 (3) branches, median simple; inner 1–3 (2) branches; outer clypeal with 1–3 (1) branches; the longest of these setae is shorter than one-half the length of the head (usually even less than one-third). Not less than 50 (30–75) scales in the comb. The branching of the setae posterior to the comb: 1–6 (3); 2–6 (5); 4–14 (10); 1–4 (2); 3–6 (4). Siphon index 1.4–2.4 (average 1.76). Siphon greatly constricted apically (coefficient of constriction 10–35, average 27.1). On the pecten, 6–16 (11) fairly long, usually simple (without denticles) pecten teeth; of these, the distal ones are set widely apart from each other and are placed not in one regular line, but descending on to the lateral surfaces of the siphon and sometimes almost reaching its apex. Posterodorsal margin of the saddle implanted with large and small spines turned outward (Fig. 30). Lateral seta of the saddle with 2–6 (3) branches; outer caudal seta with many branches (8–16, average 11); inner with one, or more often, two branches. The ventral brush has 13–18 (15) setae set on the common base and 3–6 (5) anterior to it. Dorsal gills (with index 0.6–1.4, average 0.94) somewhat longer than the ventral ones.

Pupa. Paddles relatively very broad with index (ratio of the

length to width) 96–118 (average 105.8). Outer margin of the paddle with numerous pointed denticles.

Distribution (Fig. 87). In the USSR: Ukraine, Crimea, southern Volga region, southern Ural region, Caucasus, Kazakhstan, Central Asia. Southern regions of western Siberia, England, Switzerland, southern part of the Federal Republic of Germany, Hungary, Yugoslavia, Rumania; everywhere in the Mediterranean; in Africa, in the south to Sahara, Eritrea, Somali, Sudan; not found in the equatorial forests but then southern Africa (Transvaal and others); Atlantic islands; everywhere in the Middle East and Asia Minor; in Arabia and northern India.

Biology. These are mosquitoes of forest-free regions in the plains and hills. Common in human habitations. Attack man occasionally, but the main hosts are birds. Considered as possible vectors of Malta fever; experimentally infected with the virus of western Nile encephalitis. The preimaginal stages exceptionally eurytopic; prefer moderately hypothermal or isothermal β - and α -mesosaprobic waters; found in saline waters (up to 10 per thousand); avoid heavily shaded regions. Life forms are diverse; more often polycyclic with female diapause (II) or without diapause (VIII); sometimes polycyclic with egg diapause (VI) or with diapause possibly in all growth stages (VII).

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